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# Biofacies and palaeoenvironments of conodonts in Cambro-Ordovician sequences of the Quebrada de Humahuaca, Cordillera Oriental of Jujuy, Argentina

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The taxa frequencies and cluster analysis of 10 837 conodonts recovered from the Santa Rosita Formation on the eastern flank of the Quebrada de Humahuaca, Cordillera Oriental of Argentina, were carried out for palaeoenvironmental interpretations. The first type of analysis allowed us to identify three conodont biofacies: *Variabiloconus-Teridontus*, *Utahconus-Acanthodus* and *Tilcarodus-Drepanoistodus*, and the cluster analysis helps define respective sub-biofacies. The first biofacies is not constrained to a particular environment, the second biofacies, which is characterized by typical Laurentian genera, is related to sandstones from shallow-water environments, while the third one is better represented in deeper water siliciclastic lithofacies. A nektobenthic mode of life is suggested for *Utahconus* and *Acanthodus*, but a pelagic behaviour is apparent for the rest of the taxa, well adapted to off-shore biotopes in particular cases (proto- and paraconodonts). The faunal composition reveals a mixture of Baltic and Laurentian taxa, as well as endemic forms that define the Southwestern Gondwana Province from the Cold Domain in the Shallow-Sea Realm. The presence of typical species from low latitudes (e.g. Australia) confirms the installation of an oceanic perigondwanian corridor, which was open to faunal migration during the late Cambrian-early Ordovician. Copyright © 2012 John Wiley & Sons, Ltd.

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### 1. INTRODUCTION

Palaeoecological studies of conodonts have been carried out by a number of authors since the first contributions as theoretical models in the early 1970's (e.g. Seddon and Sweet, 1971; Barnes and Fåhraeus, 1975; Ji and Barnes, 1994; Albanesi, 1998; Zhang and Barnes, 2004). They postulated different lifestyles for this fossil group, currently being accepted that some genera had a pelagic habit, while other taxa have a nektobenthic mode of life (Pohler and Barnes, 1990). However, synecological aspects of a large amount of conodont faunas from Gondwana are still unknown.

The percentage composition of genera and species, and the link between themselves and their sedimentological environment were analyzed to determine the distribution of biofacies, and to deduce the composition of the conodont communities in the palaeoenvironments of the study area. For this purpose, different graphs are presented:

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relative frequency, cluster analysis, and a three-dimensional palaeoenvironmental model proposed.

The term 'biofacies' is used in this work as an association of taxa that are recorded together in a rock whose presence has palaeoenvironmental connotations (cf. Ludvigsen *et al.*, 1986). Therefore, its relationship with the lithology and stratigraphy is extremely close, but does not necessarily reflect an ecological association. The term 'community', on the other hand, is an ecological association of taxa that lived relatively close together under particular environmental conditions (cf. Zhang and Barnes, 2004).

The studied lithostratigraphic unit corresponds to the Santa Rosita Formation and equivalent units in the Tilcara Range and Alfarcito Hills, on the eastern flank of the Quebrada de Humahuaca, in the Cordillera Oriental of Argentina (Figure 1). The age for these outcrops ranges from late Furongian to middle Tremadocian (Tr2) (late Cambrian to Early Ordovician) (Figure 2). The Santa Rosita Formation is composed of six members, from bottom to top: the Tilcara, Casa Colorada, Pico de Halcón, Alfarcito, Rupasca and Humacha members. The Tilcara and Pico de Halcón members were deposited in a fluvio-estuarine environment

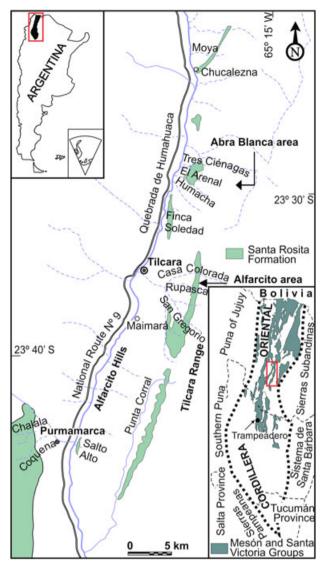


Figure 1. Location map of the study area and analyzed sections for conodont palaeoenvironments, with outcrops of the Santa Rosita Formation in light green. Map of the Argentine Cordillera Oriental, with Cambro-Ordovician outcrops in dark green. This figure is available in colour online at wileyonlinelibrary.com/journal/gj

and the remaining units were deposited under open sea conditions, in a shallow-water platform. The upper three members were productive for conodonts, consequently in this contribution we analyzed the association of conodonts from the Alfarcito, Rupasca and Humacha members. The Alfarcito Member is a heterolithic succession of siltstones and sandstones with intercalated calcarenites and coquinas. The Rupasca Member is mainly a shaly-silty unit with scarce and thin levels of sandstones and coquinas, and the Humacha Member consists of sandstones with hummocky cross-stratification and trace fossils, and scarce siltstones. Each lithostratigraphic unit is made up of transgressive—regressive cycles of different magnitude; on the other hand, the regressive cycles

are represented by sandy levels and accumulation of diverse types of bioclasts. These cycles were tentatively correlated with global transgressive–regressive events: the Basal House Lowstand (BHL), *Acerocare* Regressive Event (ARE), Black Mountain Eustatic Event (BMEE), *Peltocare* Regressive Event (PRE) and *Ceratopyge* Regressive Event (CRE) (Figure 2).

A detailed stratigraphic and palaeoenvironmental analysis of the Santa Rosita Formation has been carried out by Buatois and Mángano (2003), Mángano and Buatois (2004) and Buatois *et al.* (2006), among others. Furthermore, biostratigraphic studies for this unit were accomplished by Zeballo *et al.* (2005, 2008, 2011), and Zeballo and Albanesi (2013).

### 2. MATERIAL AND METHODS

The studied collection consists of 10 837 conodonts (see Appendix, Tables 1 and 2) from the Moya, Angosto de Chucalezna, Tres Ciénagas, El Arenal, Humacha, Casa Colorada, San Gregorio, Punta Corral and Salto Alto sections (abbreviated Moya, Chuc, TrCi, ElAr, Hum, CC, SG, PtaCorral and Purm, respectively; Figure 1). The Abra Blanca area comprises the Tres Ciénagas, El Arenal and Humacha creeks. Also, we included conodont collections from the Coquena, Chalala (Purmamarca area) and Trampeadero creeks (Parcha area) (abbreviated Coq, Chal, and Tramp, respectively), which are control sections outside the Tilcara Range (Figures 3 and 4).

In the analysis of the relative frequencies, the relative percentages of conodont genera in three of the most complete sections of the study area (El Arenal, Humacha and San Gregorio creeks) are plotted. The samples containing less than three elements are dismissed because they produce abnormal frequency peaks.

For the cluster analysis we follow the methodology used by Zhang and Barnes (2004). To this purpose, the study area is divided into two minor geographic areas: northern (including the Moya, Angosto de Chucalezna, Tres Ciénagas, El Arenal and Humacha sections) and southern (corresponding to the Casa Colorada, San Gregorio, Punta Corral, Salto Alto, Coquena, Chalala and Trampeadero sections) (Figure 1).

Double clusters were made, Q and R types (organized according to the similarity between samples or the coexistence of taxa, respectively), for the northern and southern areas. The assembly of the clusters was performed using the Paired Group or Unweighted Pair-Group Moving Average (UPGMA) algorithm and the similarity measure used was the Pearson correlation coefficient (*r*). The dendrograms were performed using the program PAST version 2.01 (Hammer *et al.*, 2001), with absolute abundances of each sample, obtained after dividing the number of elements of each species by the weight of each sample. In turn, there were created frequency intervals of <1, 1–4, 5–9, 10–24, 25–49, 50–99 and >100 conodonts/kg of rock, plotted by circles of different sizes.

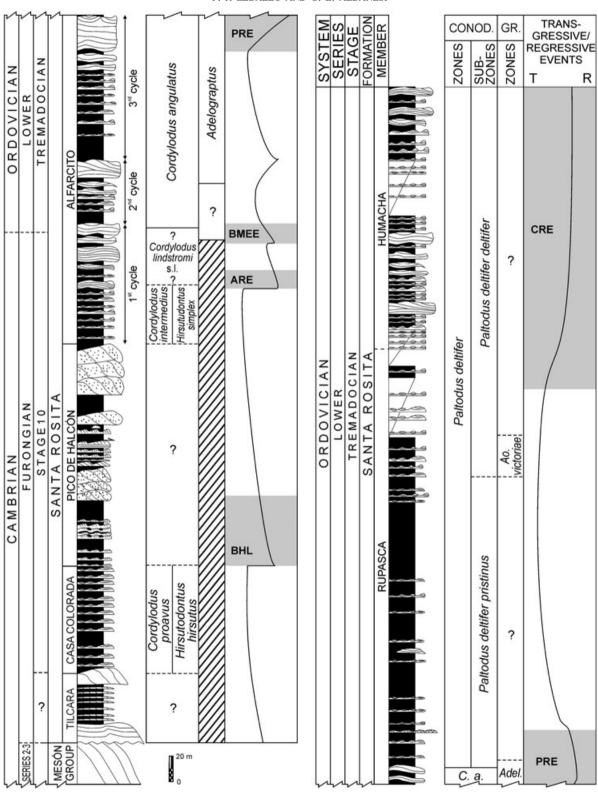


Figure 2. Composite stratigraphic column of the Santa Rosita Formation at the Tilcara Range, with transgressive–regressive cycles (after Buatois *et al.*, 2006; Zeballo *et al.*, 2005, 2011; Zeballo and Albanesi, 2009, 2013) and main eustatic events in dark grey (after Miller *et al.*, 2003, 2006, and Lehnert *et al.*, 2005) (Conod.: conodonts, Gr.: graptolites, *C. a.: Cordylodus angulatus, Adel.: Adelograptus, Ao. victoriae: Aorograptus victoriae*, BHL: Basal House Lowstand, ARE: *Acerocare* Regressive Event, BMEE: Black Mountain Eustatic Event, PRE: *Peltocare* Regressive Event, CRE: *Ceratopyge* Regressive Event). See Figure 3 for Key.

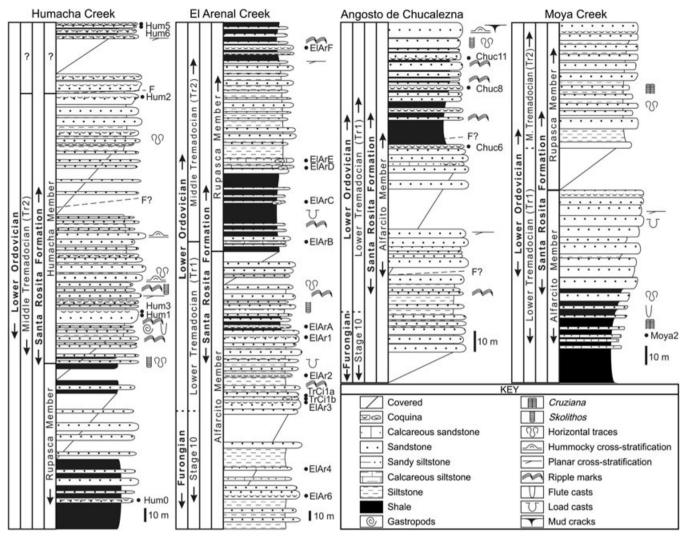


Figure 3. Stratigraphic columns of the Santa Rosita Formation in the northern area and location of the productive samples.

# 3. RELATIVE FREQUENCY OF GENERA AND RECOGNITION OF BIOFACIES

The relative frequency of genera allows to visualize the variation in the composition of conodont faunas in a single section through geological time and in correspondence with environmental changes. We selected the El Arenal and Humacha (Figure 3) and San Gregorio (Figure 4) creeks for this analysis, in the north and in the south of the study area, respectively, because they exhibit the most complete biostratigraphic records.

Figures 5 and 6 show a predominance of the genera *Variabiloconus* and *Teridontus* in the lower Alfarcito Member (samples ElAr6, TrCi1a, TrCi1b and ElAr3 in the Abra Blanca area, and samples SG1, SG2 and SG4 in the Alfarcito area), with a lower participation (*ca.* 30% in the San Gregorio section and *ca.* 20% in the El Arenal section) of the genera

Striatodontus, Cordylodus and Drepanoistodus, like protoand paraconodonts at the same levels.

From the sample ElAr1, corresponding to the top of the second transgressive–regressive cycle of the Alfarcito Member, the appearance of the genus *Utahconus* is apparent. This genus also appears in the sample SG7A, which corresponds to the top of the third cycle of the same member (Figure 2). This latest transgressive–regressive cycle shows differences between the two sections studied: in the northern section, in the sample ElArA, *Utahconus* was recorded with 35% and *Acanthodus* with 31% of the total conodont fauna, while in the southern section, the latter taxon was recorded with a very low frequency in contemporary levels, with *Utahconus* the dominant genus (67%). At the same time, *Teridontus* dramatically decreases in the El Arenal section and *Variabiloconus* does so in the San Gregorio section. These two taxa are, therefore, mutually exclusive (Figures 5 and 6).

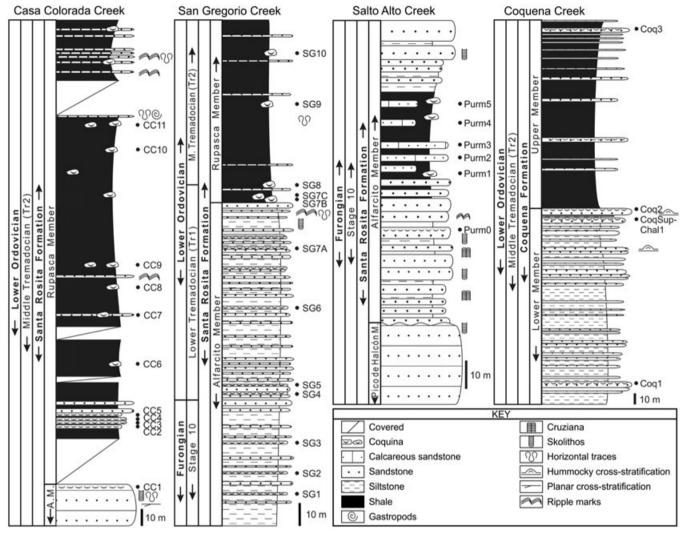


Figure 4. Stratigraphic columns of the Santa Rosita and Coquena formations in the southern area and location of the productive samples.

Relative frequency analysis also verifies the presence of other taxa in a subordinate way, such as Rossodus, Kallidontus, Ulrichodina and Phakelodus, the latter included within proto- and paraconodonts in the sample ElArA. At this level, the first appearance of *Tilcarodus* and *Paltodus* occurs, although in smaller proportion than in younger levels. The base of the Rupasca Member shows an increase in diversity of taxa in both sections, with the emergence of genera such as Drepanodus, Kallidontus, and a significant increase of Semiacontiodus in the sample SG7B. The contemporary level at the El Arenal Creek, ElArB sample, corresponds to a particular calcareous silty level, with a fauna that is only recorded in this horizon, including the genera Coelocerodontus, Filodontus and ca. 3% of Kallidontus, the highest percentage of this taxon recorded in the entire area. Also, the frequency of proto- and paraconodonts reaches ca. 10%, including the genera Granatodontus, Phakelodus and Furnishina. The

overlying levels are related to the end of the regression that occurs in the basal Rupasca Member (Peltocare Regressive Event, PRE, Figure 2), and the corresponding samples are SG7C and ElArC. The latter repeated the association of the genera Acanthodus and Utahconus, although to a lesser extent than in the upper Alfarcito Member (ca. 50% between the two taxa), while in the sample SG7C, Utahconus, with 29% of the total fauna, is followed in abundance by Semiacontiodus, with ca. 16%, although the best represented genus is *Tilcarodus*, with 34%. In both areas there has been a progressive increase in the frequency of Drepanoistodus, Tilcarodus and Paltodus in the rest of the Rupasca Member, becoming the main components of the conodont fauna. At the same time, Teridontus dominates over Variabiloconus in the middle part of this unit, while the ratio is reversed at the top. The Humacha Member is only present in the

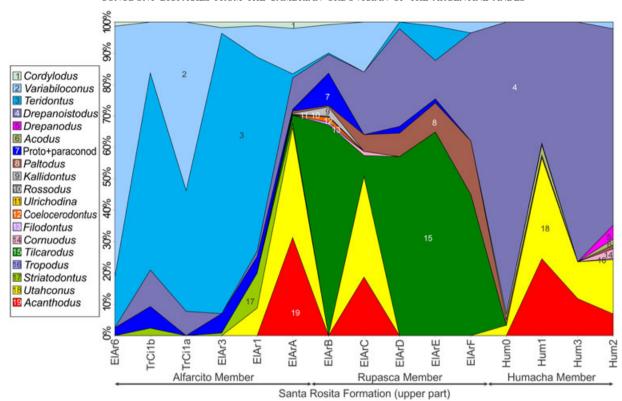


Figure 5. Relative frequencies of conodont genera recorded in the Abra Blanca area (TrCi: Tres Ciénagas, ElAr: El Arenal and Hum: Humacha creeks). *X* axis: samples in stratigraphic order (oldest to the left, ranges of the lithostratigraphic units not to scale), *Y* axis: relative frequencies (expressed in percentages).

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eponymous section of the northern area, and begins in Hum1 with the association *Acanthodus* and *Utahconus*, as recorded previously. That association reaches 73% of the total fauna, followed by *Drepanoistodus*, and minor components such as *Paltodus*, *Acodus*, *Cornuodus*, *Drepanodus*, *Tropodus* and *Variabiloconus*.

The peaks of the two most abundant genera of conodonts in Figures 5 and 6 determine assemblages defined as biofacies, although as few as one or two taxa can be present. These biofacies are (i) *Variabiloconus–Teridontus*, (ii) *Utahconus–Acanthodus* and (iii) *Tilcarodus–Drepanoistodus*. The discussion of these biofacies is presented below, together with the analysis of the whole samples and sections.

# 4. CLUSTER ANALYSIS AND RECOGNITION OF SUB-BIOFACIES

Cluster analysis verifies the occurrence of certain species associated with particular lithologies and environments, while other taxa are distributed in different types of rocks. These associations define sub-biofacies, which bear the specific names of taxa that are more abundant or characteristic of a palaeoenvironment. Moreover, samples with conodonts are grouped into clusters with similar faunal content, representing different palaeoenvironments (Figures 7 and 8). The three conodont biofacies are divided into the following respective sub-biofacies:

- (i) Variabiloconus-Teridontus Biofacies: related to diverse shallow-water environments, from shoreface to lower off-shore. It consists of three sub-biofacies: Variabiloconus datsonensis-Teridontus gallicus Subbiofacies, Variabiloconus crassus-Teridontus gallicus Sub-biofacies, and Teridontus gallicus Sub-biofacies.
- (ii) Utahconus-Acanthodus Biofacies: related to shallow-water environments (shoreface to off-shore transition). The six sub-biofacies are: Utahconus tortibasis-Acanthodus raqueli Sub-biofacies, Utahconus scandodiformis-Acanthodus humachensis Sub-biofacies, Utahconus purmamarcensis-Acanthodus raqueli Sub-biofacies, Utahconus sp.-Acanthodus raqueli Sub-biofacies, Utahconus sp.-Acanthodus sp. Sub-biofacies, and Utahconus tortibasis-Semiacontiodus spp. Sub-biofacies.
- (iii) Tilcarodus—Drepanoistodus Biofacies: related to moderate to deep-water environments (upper to lower off-shore).
   It comprises a single Tilcarodus humahuacensis— Drepanoistodus chucaleznensis Sub-biofacies.

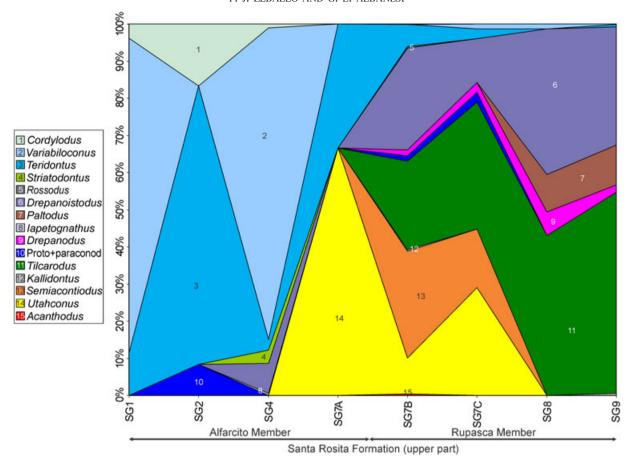


Figure 6. Relative frequencies of conodont genera recorded in the San Gregorio (SG) creek. X axis: samples in stratigraphic order (oldest to the left, ranges of the lithostratigraphic units not to scale), Y axis: relative frequencies (expressed in percentages). This figure is available in colour online at wileyonlinelibrary.com/journal/gj

# 4.1. Sub-biofacies of the Variabiloconus–Teridontus Biofacies

# 4.1.1. Variabiloconus datsonensis—Teridontus gallicus Sub-biofacies

This sub-biofacies is represented in the El Arenal section by samples ElAr6 and ElAr4, and in the Salto Alto section by samples Purm1', Purm2, Purm2', Purm3, Purm3' and Purm3", together with the samples PtaCorral3 and SG2, from Punta Corral and San Gregorio sections, respectively. It is mainly composed of Variabiloconus datsonensis (Druce and Jones) and Teridontus gallicus Serpagli, Ferretti, Nicoll and Serventi, which contribute ca. 96% in ElAr6 sample and ca. 65% in Purm3 sample, with minor participation of other taxa, e.g. Variabiloconus bicuspatus (Druce and Jones). In the 'Purmamarca Shales', Salto Alto Creek, the association consists of diverse species of Cordylodus (e.g. C. proavus Müller, C. caboti Bagnoli, Barnes and Stevens, C. cf. andresi Viira and Sergeyeva), although with a very low proportion. Hirsutodontus galerus Tolmacheva and Abaimova and Hirsutodontus simplex (Druce and Jones) are recorded in this section, as well as the highest frequency of para- and protoconodonts of the study area, such as *Albiconus postcostatus* Miller, *Phakelodus elongatus* (Zhang), *P. tenuis* (Müller), *Problematoconites perforatus* Müller and *Westergaardodina polymorpha* Müller and Hinz. The environment to which this sub-biofacies is related is lower to upper off-shore, and eventually shelf.

# 4.1.2. Variabiloconus crassus—Teridontus gallicus Subbiofacies

This sub-biofacies is identified in the uppermost levels of the Alfarcito Member, in samples TrCi1a, TrCi1b, ElAr1, Chuc6, Chuc8, Chuc11 and Moya2, of the northern area, and in samples CC2, CC3, CC5 and SG4, from the southern area, together with Tramp3. Together with the nominal taxa, the species *Cordylodus angulatus* Pander, *Drepanoistodus alfarcitensis* Zeballo, Albanesi and Ortega, *Problematoconites perforatus*, *Semiacontiodus minutus* Zeballo, Albanesi and Ortega, *Striatodontus* sp. and *Utahconus* sp., are associated in a significant number. *Variabiloconus crassus* Zeballo and Albanesi plus *Teridontus gallicus* compose *ca.* 93% of the

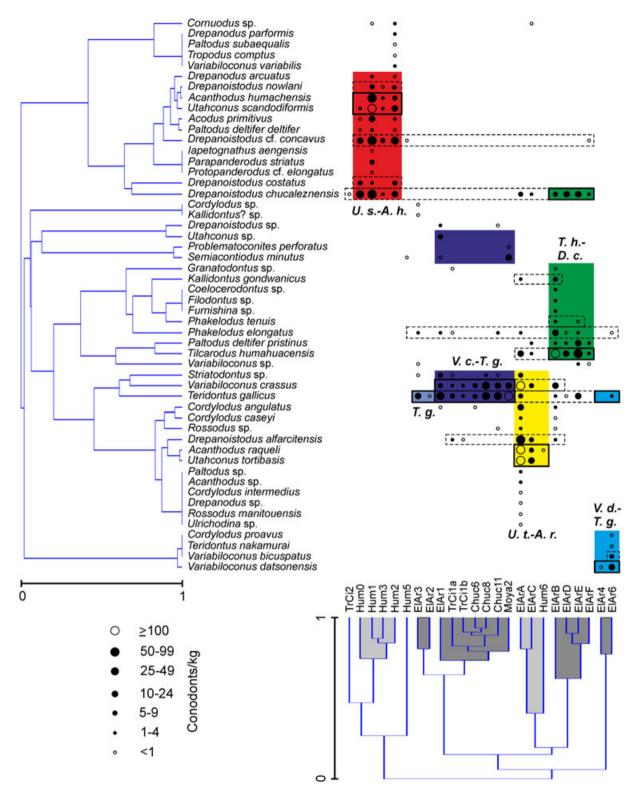


Figure 7. Cluster analysis of the northern area (*U. s.-A. h.: Utahconus scandodiformis–Acanthodus humachensis* Sub-biofacies, *V. c.-T. g.: Variabiloconus crassus–Teridontus gallicus* Sub-biofacies, *U. t.-A. r.: Utahconus tortibasis–Acanthodus raqueli* Sub-biofacies, *T. h.-D. c.: Tilcarodus humahuacensis–Drepanoistodus chucaleznensis* Sub-biofacies, *V. d.-T. g.: Variabiloconus datsonensis–Teridontus gallicus* Sub-biofacies). This figure is available in colour online at wileyonlinelibrary.com/journal/gj

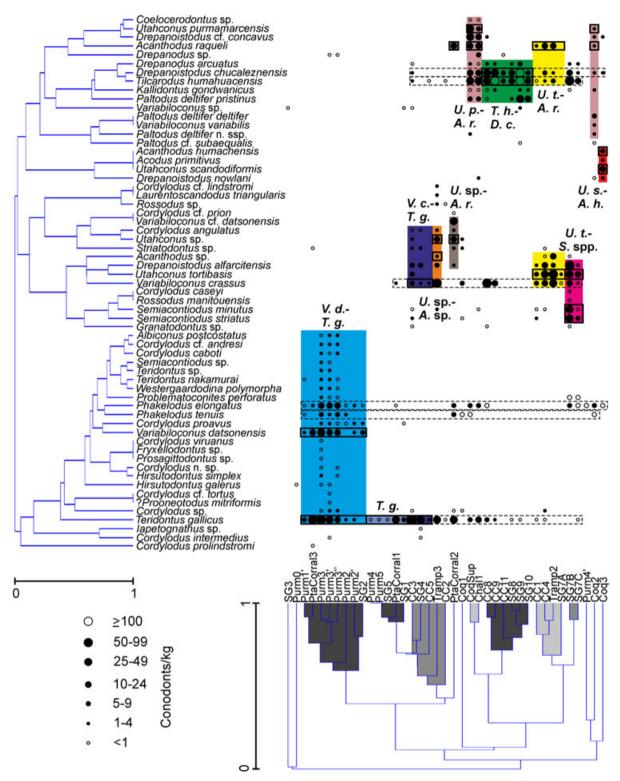


Figure 8. Cluster analysis of the southern area (*U. s.-A. h.: Utahconus scandodiformis–Acanthodus humachensis* Sub-biofacies, *V. c.-T. g.: Variabiloconus crassus–Teridontus gallicus* Sub-biofacies, *U. t.-A. r.: Utahconus tortibasis–Acanthodus raqueli* Sub-biofacies, *T. h.-D. c.: Tilcarodus humahuacensis–Drepanoistodus chucaleznensis* Sub-biofacies, *V. d.-T. g.: Variabiloconus datsonensis–Teridontus gallicus* Sub-biofacies, *U. sp.-A. r.: Utahconus* sp.-Acanthodus raqueli Sub-biofacies, *U. t.-S.* spp.: *Utahconus tortibasis–Semiacontiodus* spp. Sub-biofacies, *U. p.-A. r.: Utahconus purmamarcensis–Acanthodus raqueli* Sub-biofacies). This figure is available in colour online at wileyonlinelibrary.com/journal/gj

fauna in sample Moya2, in the northern area, and ca. 68% in sample CC3, in the southern area. The samples belonging to this sub-biofacies come from a variety of lithologies, which were deposited from shoreface to lower off-shore.

## 4.1.3. Teridontus gallicus Sub-biofacies

This third sub-biofacies of the Variabiloconus-Teridontus Biofacies is identified in the samples ElAr3, ElAr2 from the northern area, and samples SG1, SG5, PtaCorral1, Purm4 and Purm5 from the southern area. The diversity of taxa found is the lowest of all sub-biofacies of the study area, with Teridontus gallicus being the dominant taxon, followed by a low frequency of Phakelodus elongatus, Cordylodus proavus, Variabiloconus crassus and Variabiloconus sp. The depositional environment is lower to upper off-shore. Although the sample ElAr3 was obtained from the top strata of the lower Alfarcito Member, it corresponds to a lens of calcarenite interbedded between sandstone that could have come from deeper levels of the basin.

### 4.2. Sub-biofacies of the Utahconus-Acanthodus Biofacies

#### 4.2.1. Utahconus tortibasis-Acanthodus raqueli Subbiofacies

Within the Utahconus-Acanthodus Biofacies, this subbiofacies is distinguished by the nominal taxa which represent ca. 50% of the total fauna, followed by Variabiloconus crassus, Tilcarodus humahuacensis (Albanesi and Aceñolaza), Drepanoistodus alfarcitensis, D. chucaleznensis Albanesi and Aceñolaza and Cordylodus angulatus. In a lower proportion Teridontus gallicus, Phakelodus elongatus and Paltodus deltifer pristinus (Viira), are recorded. The samples related to this sub-biofacies are ElArA, ElArC and Hum6, in the northern area, and CC1, CC4, SG7A and Tramp2 in the southern area; the environment where these rocks were deposited is shallow, from shoreface to off-shore transition, corresponding to sandstones with hummocky crossstratification structures from the third cycle of a transgressive-regressive interval of the Alfarcito Member, and to the regressive event in the lower part of the Rupasca Member. The sample ElArC probably has some reworked specimens from nearshore environments, since it intercalates with lower off-shore shales.

#### 4.2.2. Utahconus scandodiformis-Acanthodus humachensis Sub-biofacies

This sub-biofacies is another shallow-water association (shoreface to off-shore transition) which is also recorded in the sandstones of the Humacha Member. Such a biofacial unit is located in the samples Hum0, Hum1, Hum2, Hum3, from the Humacha Creek and the sample Coq3, in the Coquena Creek. The species Utahconus scandodiformis Zeballo and Albanesi and Acanthodus humachensis Zeballo and Albanesi combined represent ca. 55% of the total fauna in the sample Hum1, with an important proportion of the genus Drepanoistodus (reaching 38%), through the species D. chucaleznensis, D. cf. concavus (Branson and Mehl), D. costatus (Abamoiva) and D. nowlani Ji and Barnes. The index fossil Paltodus deltifer deltifer (Lindström) and the species Acodus primitivus Zeballo and Albanesi are found represented proportionally in a lower amount, as well as other taxa, such as Cornuodus sp., Drepanodus arcuatus Pander, D. parformis Löfgren and Tolmacheva, Parapanderodus striatus (Graves and Ellison), and Variabiloconus variabilis (Lindström).

# 4.2.3. Utahconus purmamarcensis-Acanthodus raqueli Sub-biofacies

This sub-biofacies is recorded to the west of the study area, in the Coquena and Chalala creeks (samples CoqSup, Coq2 and Chal1). Utahconus purmamarcensis Zeballo and Albanesi and Acanthodus raqueli Zeballo and Albanesi are represented with ca. 32% of the fauna in the sample CoqSup, while the absolute frequency of Tilcarodus humahuacensis and Drepanoistodus spp. (D. chucaleznensis, D. cf. concavus and D. nowlani) is significant. Teridontus gallicus, Paltodus deltifer ssp. (P. d. pristinus, P. d. deltifer and P. deltifer n. ssp.) and Phakelodus elongatus are recorded, although with lower percentages than the mentioned taxa. The samples are coquinas from interbedded sandstone strata of shallow-water deposits (shoreface) that occur at the top part of the lower member of the Coquena Formation.

4.2.4. Utahconus sp.—Acanthodus raqueli Sub-biofacies This sub-biofacies is also related to another regressive event, but from the top of the lower interval of the Alfarcito Member, the level PtaCorral2 that was sampled in the Punta Corral Creek. It represents the oldest record of the Utahconus-Acanthodus Biofacies. The species that accompany Utahconus sp. and Acanthodus raqueli are Variabiloconus cf. datsonensis, Teridontus gallicus, Striatodontus sp., Cordylodus angulatus, and in a lower proportion Drepanoistodus alfarcitensis, Phakelodus elongatus. P. tenuis and Cordylodus cf. prion Lindström.

# 4.2.5. *Utahconus* sp.-*Acanthodus* sp. *Sub-biofacies* This sub-biofacies is present in sample Tramp3, from the Trampeadero section. The association is composed of the nominal taxa, together with Variabiloconus crassus, Teridontus gallicus and Drepanoistodus alfarcitensis, while Cordylodus

cf. lindstromi Druce and Jones, Laurentoscandodus triangularis (Furnish) and Semiacontiodus minutus appear scarcely in this association.

# 4.2.6. Utahconus tortibasis—Semiacontiodus spp. Subbiofacies

In the San Gregorio Creek, in the upper interval of the Alfarcito Member (SG7B and SG7C), is recorded the association *Utahconus tortibasis* Zeballo and Albanesi with *Semiacontiodus minutus* and *Semiacontiodus striatus* Zeballo, Albanesi and Ortega, which give the name to the sub-biofacies. The latter genus reaches 29% of the conodont fauna in the sample SG7B, followed in lower proportion by *Drepanoistodus* (*D. alfarcitensis* and *D. chucaleznensis*) and *Tilcarodus humahuacensis*, and the remaining *Utahconus tortibasis* with *ca.* 10%. The relationship is reversed in the sample SG7C, where this taxon represents 29% and *Semiacontiodus minutus* + *S. striatus* combined only constitute 16% of the total fauna. This biofacial unit is not found currently in other sections.

# 4.3. Sub-biofacies of the Tilcarodus-Drepanoistodus Biofacies

# 4.3.1. The Tilcarodus humahuacensis—Drepanoistodus chucaleznensis

This sub-biofacies is the only sub-unit of the Tilcarodus-Drepanoistodus Biofacies, for which the description of both is convergent. Although Tilcarodus humahuacensis and Drepanoistodus chucaleznensis are also recorded in other sub-biofacies, in this biofacies they represent the highest percentages (86% in sample SG9 and 77% in sample ElArE). Some associated species are Coelocerodontus sp., Cordylodus angulatus, C. caseyi Druce and Jones, Drepanodus arcuatus, Kallidontus gondwanicus Zeballo and Albanesi, Paltodus deltifer pristinus and Granatodontus sp., among others, as well as Variabiloconus crassus and Teridontus gallicus, which are also present in the previously mentioned sub-biofacies. It is particularly interesting to note the faunal composition in the sample ElArB (the calcisilt-rich strata intercalated in the basal Rupasca Member), at El Arenal Creek, with a significant increase of para- and protoconodonts (e.g. Phakelodus elongatus, P. tenuis, and Furnishina? sp.). The euconodont Filodontus sp. is recorded with scarce elements only in this sample, while the genera Utahconus and Acanthodus which characterize the homonymous biofacies, are not recognized herein, but they occur in the underlying and overlying levels, revealing a sharp environmental change in this stratigraphic interval. The palaeoenvironment, as suggested by the lithofacies, is shelfal to off-shore.

# 5. BIOFACIAL INTERPRETATION: CONODONT COMMUNITIES

From the observations made in the above figures, it appears that the genera *Variabiloconus* and *Teridontus* would be

pelagic in life habit, probably epipelagic, as they were recovered from coquinas and calcarenites interbedded in a wide variety of rocks, deposited in shoreface to lower offshore settings. In turn, the relationship between the two taxa is antithetical, i.e. at the same time the percentage of a genus increases while the other one decreases. This fact is more evident in the upper part of the Alfarcito Member and in the lower part of the Rupasca Member at the El Arenal and San Gregorio creeks, respectively. The water depth appears to be the controlling factor in a relationship where Teridontus occupy a more distal position than Variabiloconus. Zhang and Barnes (2004) found a similar antithetical relationship between Teridontus nakamurai (Nogami) and Phakelodus tenuis, where Teridontus dwell in shallower waters than Phakelodus, a protoconodont of pelagic habit, in preference to deeper and/or more distal water (slope). Therefore, the segregation from the coast to offshore of these taxa would be: Variabiloconus-Teridontus-Phakelodus (the latter also associated with paraconodont taxa) (Figure 9).

The dominant biofacies in the lower-half of the Alfarcito Member is that of *Variabiloconus–Teridontus*, with no observed nektobenthic communities, probably due to a high sea level and conditions of oxygen restriction on the bottom. Mángano *et al.* (2005) noted that often the sediments deposited during maximum flooding events are associated with low oxygen conditions in the environment. The presence of black shales deposited under dysoxic conditions occur at the basal Alfarcito Member in the Salto Alto section, where they would have occurred at the maximum flooding levels of the unit.

Moreover, the upper part of the Alfarcito Member and the regressive episode at the base of Member Rupasca are dominated by the Utahconus-Acanthodus Biofacies. This biofacies is recurrent and is confined to regressive episodes in the study area, and also identifies sandstones in the top of both members of the Coquena Formation, in the Humacha Member, the Devendeus Formation and, exceptionally, in the top of the lower interval of the Alfarcito Member, at Punta Corral section. Utahconus and Acanthodus species from the various sub-units of the biofacies occur in chronostratigraphic order (Utahconus sp.-U. tortibasis-U. purmamarcensis-U. scandodiformis and Acanthodus sp.-A. raqueli-A. humachensis) and are closely linked, implying that both genera would have had a nektobenthic habit, occupying a biotope of warm and shallow water near the coast. The preference of this assemblage for the shallow-water environments and its life habit is evidenced in contemporaneous levels at the Paltodus deltifer pristinus Subzone: the Utahconus-Acanthodus Biofacies only is present in sandy-regressive levels of the uppermost Lower Member of the Coquena Formation, while it is absent in deeper water strata of the Rupasca Member, Santa Rosita Formation. The Alfarcito area sections and particularly the San Gregorio section (to the south), have deeper-water lithofacies than those recorded in the Abra Blanca area (to the north),

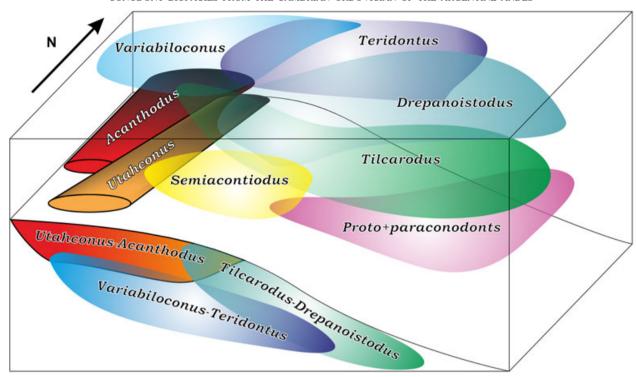


Figure 9. Palaeoenvironmental 3D model, displaying the spatial distribution of the main conodont genera recorded in the study area, at the Lower–Middle Tremadocian boundary. Upper part of the diagram with solid contour: are the nektobenthic conodont communities, without contour are the pelagic communities, lower diagram: conodont biofacies from shallow to deep water (not to scale). This figure is available in colour online at wileyonlinelibrary.com/journal/gj

where both Acanthodus and Utahconus are present. Incidentally, the R type clustering of Figure 7 (northern area) show a better association of Utahconus-Acanthodus, while the *Tilcarodus–Drepanoistodus* cluster is well represented in Figure 8 (southern area), reinforcing the association of these taxa to opposite lithofacies (shallower vs. deeper water environments). An exception to this association is in the San Gregorio Creek, in the basal strata of the Rupasca Member, where Utahconus tortibasis is associated with Semiacontiodus minutus and S. striatus, where Acanthodus is virtually nonexistent. The sample SG7B, with the Sub-biofacies Utahconus tortibasis-Semiacontiodus spp., is linked precisely to the largest transgressive event of the Santa Rosita Formation (and to the beginning of the deposition of the Rupasca Member; Figure 2) with a high concentration of organic matter and dysoxic conditions, to which Acanthodus could not adapt. Therefore, it follows that the genus Semiacontiodus would be pelagic (for unrestricted distribution), but with tolerance and/or preference for oxygen-deficient conditions, to which Acanthodus could not adapt. This inference would be reinforced by the significant increase of Semiacontiodus minutus in a calcarenite (distal tempestite, storm bed accumulation) associated with black shales in the Moya Creek (Moya2 sample).

*Drepanoistodus* is widely distributed in all lithofacies, so it would have pelagic habits, living probably near the water

surface (cf. Zhang and Barnes, 2004). Moreover, the new genus *Tilcarodus*, although also recorded in shallow-water environments, exhibits a marked increase seaward and south of the study area (Figure 9), where there is also a major deepening. Both taxa give the name to the biofacies, which characterizes the middle and upper Rupasca Member.

Finally, the proto- and paraconodonts are grouped into a unique community, because its components have a rather similar behaviour. It includes: *Phakelodus*, *Albiconus*, *Fryxellodontus*, *Furnishina*, *Problematoconites*, *Prosagittodontus* and *Westergaardodina*. One of the most common taxa of this group is *Phakelodus*, a cosmopolitan taxon found in a variety of facies from shallow-water environments, platform margins, slopes, but is mainly associated with black shales deposited under anoxic conditions, where only pelagic faunas inhabit (Miller, 1984). Consistent with the foregoing, in the study area, the community of proto- and paraconodonts presents a significant increase to the distal platform, such as in samples from the Salto Alto section and the base of the Rupasca Member. At the same time, there is an increase in this community to the south of the study area, where the lithofacies reflect a greater depth of the basin.

Figure 9 shows an approximate three-dimensional projection of the communities previously mentioned above, during the Lower–Middle Tremadocian (Tr1/Tr2) boundary interval, and its relationship with the recorded biofacies.

#### 6. PALAEOBIOGEOGRAPHY

In the basin of northwestern Argentina, is evident a mixed conodont faunal composition (Ortega and Albanesi, 2005). The index taxa identified in the area, e.g. *Paltodus deltifer* sspp., belong to the Cold Domain (low diversity and high abundance of conodonts, within which the Balto–Scandian Province is included) lacking or with exiguous amount of typical Tremadocian taxa such as *Clavohamulus*, *Loxodus* or *Rossodus* from the Tropical Domain (high diversity and endemism, within which the Laurentia, Australia and North China provinces are involved, *sensu* Zhen and Percival, 2003). Most of the genera present in the study area are cosmopolitan, e.g. *Drepanoistodus*, *Teridontus*, *Phakelodus* and *Variabiloconus*. At the same time, the new genus *Tilcarodus*, probably endemic to the western edge of Gondwana, is recorded. An important contribution of taxa

characteristic of the Tropical Domain are recognized for the first time in the basin, through the genera *Utahconus* and *Acanthodus*, albeit with new species, typical of Gondwana (Zeballo and Albanesi, 2013). Therefore, the conodont fauna of the Cordillera Oriental can be referred to a new palaeobiogeographic unit, the Southwestern Gondwana Province, within the Cold Domain of the Shallow-Sea Realm, located at middle latitudes (following the model of Zhen and Percival, 2003; see also Albanesi *et al.*, 2007).

Various palaeogeographic reconstructions located the Cordillera Oriental at mid- to high latitudes during the Furongian–Early Ordovician, around 30°S latitude (e.g. Scotese and Barrett, 1990; Cocks and Torsvik, 2002; Álvaro *et al.*, 2007, 2008) (Figure 10). In turn, Vaccari *et al.* (2006) and Benedetto and Vaccari (in Benedetto *et al.*, 2007) recognize that certain forms of trilobites recorded in the Cordillera Oriental and Argentine Puna, as *Onychopyge* from the

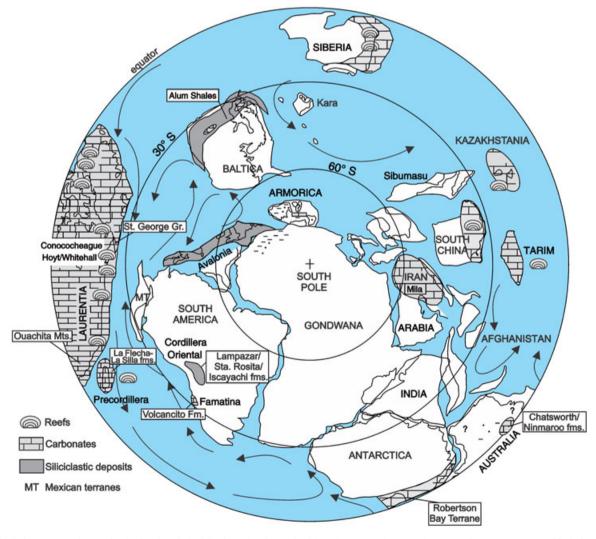


Figure 10. Palaeogeographic map for the Cambro-Ordovician boundary interval, with study areas and proposed patterns of ocean current (modified after Jell *et al.*, 1984, Benedetto, 2003, and Álvaro *et al.*, 2008). This figure is available in colour online at wileyonlinelibrary.com/journal/gj

Furongian-basal Ordovician, are also present in northern and southern China, Australia, New Zealand and Mexico, suggesting a probable linkage between these areas. Work by other authors such as Jell (1985) and Webby et al. (2000) also point in this direction, noting the affinities between the faunas of Australian-New Zealand trilobites and northern Argentina from the record of the genera Onychopyge and Australoharpes; in turn, these faunal similarities also occur among the trilobites of the Cordillera Oriental and western Argentine Puna (Benedetto et al., 2009). In a palaeogeographic reconstruction for the early Floian, Benedetto (2003) proposed a model of ocean circulation that would explain the exchange of faunas from Australasia to North Africa. Jell et al. (1984) were the first to identify this migration route through the dispersal of the gastropod Peelerophon oehlerti (Bergeron), which is present from the tropical terranes near to the southeastern Gondwanan platform (South China, Thailand (Sibumasu) and Tasmania) to the siliciclastic temperate to cold water platform in western Gondwana (Cordillera Oriental and southwestern France).

Furthermore, the conodont species *Variabiloconus datsonensis* and *V. bicuspatus* have been documented originally by Druce and Jones (1971) in rock successions of northeastern Australia (Ninmaroo Formation), and later in Antarctica (Robertson Bay Terrane) by Buggisch and Repetski (1987). Associated with these two taxa at the base of the Alfarcito Member is recorded *Hirsutodontus simplex*, a taxon that is also recorded from low palaeolatitudes (e.g. Australia, western United States, Siberia, northern China), as *H. galerus*, a newly recognized species in the Siberian platform by Tolmacheva and Abaimova (2009).

The geographic distribution of these taxa reinforces the proposal of a peri-Gondwanian ocean current from tropical latitudes to higher latitudes (cf. Aceñolaza and Lech, 1992; Benedetto, 2003), which contributed to faunal exchange along the continental margin, producing a mixture of faunas observed in the study area during the Furongian–Early Ordovician.

Recently, Albanesi and Bergström (2010) examined the palaeobiogeography of the Early–Middle Ordovician by cluster analysis (presence/absence of species) in various regions globally. During the *manitouensis–deltifer* interval, when the upper Santa Rosita Formation was deposited, two well-defined groups of clusters are evident; one gathering much of the North American basins (e.g. Ouachita Mountains, Ibex Area, and St. George Group) with the Argentine Precordillera (Figure 10), while the remaining group includes the Baltic basins and the western Gondwanian basins (Cordillera Oriental and Famatina). By the observed pattern, the authors verify that the Argentine Precordillera represents an exotic terrane with respect to the Gondwanian margin, and that during this period it has

more affinities with the Laurentian Province of the Tropical Domain. By contrast, the Cordillera Oriental is in the same cluster with localities of the Balto–Scandian Province from the Cold Domain and the Famatina System, and sections of the Cow Head Group, Newfoundland, possibly due to sampling bias or differentiation of biofacies, rather than vicariance.

### 7. CONCLUSIONS

Through graphs of generic frequency three conodont biofacies: Utahconus-Acanthodus, Variabiloconus-Teridontus and Tilcarodus-Drepanoistodus have been recognized. The first is restricted to shallow-water environments and the third is linked to moderately deep to deep-water environments. On the other hand, the Variabiloconus-Teridontus Biofacies is not confined to a particular environment, and is recorded in the absence of the above biofacies. In turn, cluster analysis has identified the Utahconus sp.-Acanthodus raqueli, Utahconus sp.-Acanthodus sp., Utahconus tortibasis-Acanthodus raqueli, Utahconus purmamarcensis-Acanthodus raqueli, Utahconus scandodiformis-Acanthodus humachensis, Variabiloconus datsonensis-Teridontus gallicus, Variabiloconus crassus-Teridontus gallicus, Teridontus gallicus and Tilcarodus humahuancensis-Drepanoistodus chucaleznensis sub-biofacies as integral parts of the biofacies above.

Overall, the frequency ratio between *Variabiloconus* and *Teridontus* is antithetical. The proportion of elements for the first taxon is higher in samples from shallow-water environments, unlike the second taxon, whose frequency increases in samples from deeper-water environments. It is postulated that there was a pelagic mode of life for these forms, with *Variabiloconus* being closer to the coast than *Teridontus*, although there were abnormal situations with opposite frequency ratios for these environments.

Acanthodus and Utahconus would have had a nektobenthic mode of life in a temperate, shallow-water biotope near the coast, and Acanthodus disappears in a north to south direction (from El Arenal and Humada creeks to San Gregorio Creek), indicating a deepening of the basin. Moreover, Tilcarodus and Drepanoistodus being pelagic, have an increased frequency in deeper waters, such as the species grouped sensu formae in proto- and paraconodonts.

The base of the Rupasca Member represents a stratigraphic interval under peculiar palaeoenvironmental conditions. In a sample from the base of the Rupasca Member at the El Arenal Creek it was noted the absence of the *Utahconus–Acanthodus* biofacies, which is documented both below and above this level. This could be linked to the onset of a transgression and the displacement of faunas to other shallower water areas of the basin.

The conodont faunas show Baltic affinities, particularly the index taxa of the identified biozones. However, certain typically Laurentian genera such as *Acanthodus* and *Utahconus* are recorded in the shallower parts of the sequences, revealing a mixture of faunas from both regions. Other taxa such as *Tilcarodus* would be endemic forms in the Argentine Cordillera Oriental so far. The faunal association represents a new palaeobiogeographical province, the Southwestern Gondwana Province within the Cold Domain of the Shallow-Sea Realm in middle latitudes.

Some species, such as *Hirsutodontus galerus*, *H. simplex*, *Variabiloconus datsonensis* and *V. bicuspatus*, recognized only in low palaeolatitudes (Australia, United States, northern China and Siberia), were documented in the study area. These records, together with the trilobite *Onychopyge* and gastropod *Peelerophon oehlerti* in the Cordillera Oriental, confirm the existence of a perigondwanian corridor that would have allowed the connection between the Australian–New Zealand faunas and the northern Argentine faunas with those from the tropical regions farther away.

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APPENDIX

Hum6 2430 Hum3 - 5 ω 10 2 2 2 46 25 15 115 99 က 347 210 11 27 170 34 23 Hum0 1100 36 **TrCi2** 3150 2 2 7 1 27 7 **EIArF** 3355 13 ω 7 2 **EIArE** 1795 28 25 148 21 7 7 **ElArD** 2830 29 7 53 **EIArC** 1565 4 4 24 **EIArB** 2870 560 376 19 2 16 0 4 -9 3 36 7 3 20 **ElArA** 2275 3 3 505 2 141 21 10 21 46 568 238 6 ~ ო **EIAr1** 2440 1 19 105 15 17 7 က 6 Table 1. Absolute frequency of conodont species from the northern area **EIAr2** 2480 7 **EIAr3** 4660 101 \_ **EIAr4** 1765 **EIAr6** 4170 7 22 2 28 2 67 45 **Chuc6** 1740 13 7 29 44 SAMPLES Mass [gr] anoistodus chucaleznensis epanoistodus nowlani epanoistodus cf. concavus epanoistodus sp. anoistodus alfarcitensis riabiloconus datsonensis riabiloconus bicuspatus ordylodus caseyi ordylodus intermedius ordylodus proavus panoistodus costatus etognathus aengensis Itodus deltifer pristinus llidontus gondwanicus apanderodus striatus topanderodus cf. elor iiacontiodus minutus carodus humahuacen abiloconus variabilis illidontus? sp. iltodus deltifer deltifer riabiloconus crassus ssodus manitouensis nakelodus elongatus nakelodus tenuis panodus parformis Itodus subaequalis eridontus gallicus eridontus nakamurai rdylodus angulatus epanodus arcuatus TOTAL elocerodontus sp. thodus raqueli anatodontus sp. odus primitivus nthodus huma iatodontus sp. panodus sp. nthodus sp. dylodus sp. ichodina sp. muodus sp. odontus sp. mishina sp. ssodus sp.

ramp3 825 - 2 24 19 ∞ 9 ~ ° 4 23 2 2 11 62 2 19 က 22 9 170 290 0 က 22 \_ en 31 34 2 4 2 2 - = 9 22 39 8 8 2 140 24 35 2 16 7 6 22 12 19 282 2 88 40 117 2 22 Ξ 8 2 3 11 2 2 8 11 4 2 - 6 6 6 4 \_ 13 47 3 78 10 67 38 46 156 33 6 9 - 9 -5 Absolute frequency of conodont species from the southern area 47 2 7 co 4 2 13 3 83 2 7 49 -2 ₩ 4 - -7 7 3 33 5 249 4 2 4 385 158 12 3 က 7 7 5 53 32 2 9 2 2 9 9 ကတ - -33 œ ariabiloconus cf. datsonensis ariabiloconus sp. entoscandodus triangularis roblematoconites perforatus "Prooneotodus" mitriformis rosagittodontus sp. pistodus cf. concavus apanodus sp. apanoistodus alfarcitensis fariabiloconus crassus fariabiloconus datsonensis Resodus sp.
Remiacontiodus minutus
Remiacontiodus striatus
Semiacontiodus sp. tahconus scandodiform todus cf. subaequalis hakelodus elongatus hakelodus tenuis ariabiloconus variabilis ryxellodontus sp. sranatodontus sp. iirsutodontus galerus lirsutodontus simplex todus deltifer n. ssp. coelocerodontus sp. cordylodus angulatus tognathus sp. anthodus sp. Fable 2.

PtaC = Punta Corral section.

TOTAL