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## Paleoecological and paleobiogeographic considerations of Ordovician graptolites from the Cordillera Oriental, Jujuy Province, Argentina

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We analyse new paleoecological data from South American graptolite records to understand the patterns that influence the space-tempo distribution of the group. A cluster analysis including taxa from the *Baltograptus* cf. *B. deflexus* and *Didymograptellus bifidus* Zones is carried out to evaluate the paleogeographic relationships between north-western Argentina and the other regions in the world. Three different biofacies were recognised in the Acoite Formation. The first biofacies takes place in the lower part of the unit, corresponding to pelitic levels (*Tetragraptus phyllograptoides* and *Tetragraptus akzharensis* Zones), and it is represented by pandemic forms. The other two biofacies belong to the endemic or neritic shallow water environments, and develop in deposits corresponding to the middle part of the Acoite Formation (bottom of the *Baltograptus* cf. *B. deflexus* Zone) in the Sierra de Aguilar, and in the upper half of the unit exposed in the Los Colorados area (*D. bifidus* Zone), respectively. The statistical analysis highlight the paleobiogeographic relationship between north-western Argentina and south-western China during the middle-upper Floian (*Baltograptus* cf. *B. deflexus* and *D. bifidus* Zones), and it supports the hypothesis that during the Early Ordovician north-western Argentina was located in the middle to high latitudes, included in the cold water faunal realm.

**Keywords:** Ordovician; graptolites; biofacies; paleoenvironmental; paleobiogeography

### Introduction

Graptolites are marine macrofossils, traditionally considered to be an important tool for establishing biostratigraphic correlations of regional and international Paleozoic sedimentary facies (Webby et al. 2004; Zalasiewicz et al. 2009; Zhang et al. 2010). In addition, recent studies postulate that many taxa are useful as indicators of paleoenvironmental changes too (Egenhoff and Maletz 2007; Cooper et al. 2012). However, paleoecological studies of graptolites from north-western Argentina are very scarce, and due to that the main goal of this study is to contribute to the understanding of paleoecological patterns that influence the distribution of the group, based on new data from the Sierra de Aguilar (Cordillera Oriental) and complementary bibliographic information produced during the last decade. Moreover, the statistical analysis recently presented by the authors (Vento et al. 2012 and references mentioned therein) to determine the paleobiogeographic relationship between north-western Argentina, Baltoscandia, Great Britain, south-western China and North America is now completed with new records of the middle and upper Floian taxa.

To understand the spatial and temporal distribution of the faunal assemblage, it is necessary to understand the behaviour of each of the species and analyse their

relationships with the environment in which they lived. This fact is reflected in the typical characteristics of those individuals who coexist in one place and time, which are more difficult to identify from the study of a particular fossil group, which became extinct millions of years ago. However, graptolites were organisms that had a worldwide distribution and are preserved in a wide range of sedimentary facies (Bulman 1964). In consequence, some distribution patterns have been established.

Among the factors that contribute to the spatial differentiation of the graptolite faunas, Cooper et al. (1991) considered ocean currents and watermass specificity (Williams 1969; Bulman 1971, 1978; Berry 1974; Erdtmann 1976, 1984), latitudinal surface water temperature gradients (Bulman 1964, 1971; Skevington 1973, 1974, 1976), depth distribution (Ross 1961; Berry 1962) and, finally, the partitioning of shelf and oceanic water masses (Raymont 1983). The lateral differentiation of specific water masses together with the depth enables to establish two essential habitats for graptolites assemblage: first, the shallow water biotope, where both forms of epipelagic, pandemic (in oceans and continental margins) and the epipelagic, endemic (restricted, in this case, to the inner shelf areas) are associated and, second, the deep water biotope, with a clear predominance of the mesopelagic conical to branched

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colonies of cosmopolitan distribution (Cooper et al. 1991; Cooper 1998). The majority of graptolites were pandemic and not subject to latitudinal limitation in their distribution, even at times of greatest provincialism. Most pandemic species lived in the epipelagic zone and must, therefore, have been tolerant of a wide range of temperature (eurythermal); however, other species showed considerable sensitivity to temperature differences (stenothermal) (Cooper et al. 1991).

### Location and geological framework

The Sierra de Aguilar and the Los Colorados regions are two classical areas to study the lower Paleozoic sequence in north-western Argentina. Both regions are located in the Jujuy Province and correspond to the western flank of the Argentinian Cordillera Oriental (Figure 1). This geological province is located in the southern Central Andean Basin of South America, and according to recent studies it evolves as a forebulge depozone of the extended Ordovician foreland basin system developed in north-western Argentina (Bahlburg and Furlong 1996; Astini 2003).

Early Ordovician platform sediments of the Cordillera Oriental are characterised by black and grey shales and siltstones interbedded with fine- to medium-grained

sandstones towards the top of the sequence of the Santa Victoria Group (Upper Cambrian-Ordovician), which on the western flank of the Cordillera Oriental is mainly represented by the Santa Rosita and Acoite Formations, and it is separated from the underlying Mesón Group by the Irúyica discordance.

According to recent geotectonic models, the sedimentation process in the Acoite Formation occurred on a low-angle marine ramp in the peripheral bulge basin, corresponding to the Cordillera Oriental, with volcanoclastic sediment from the arch located to the west and deltaic fans developed eastward into the foreland (Astini 2003, 2008). The unit is constituted by clastic material deposited in a high-rate sedimentation platform, shows an upward coarsening sequence with deltaic influence to the top and it is extensively exposed on the western flank of the Cordillera Oriental (Astini and Waisfeld 1993; Waisfeld 1993).

Los Colorados area is located to the west of the saline lagoon of Salinas Grandes and approximately 80 km to the south of the Sierra de Aguilar (Figure 1). Lower and middle Paleozoic strata are widely exposed in the region, and the stratigraphic relations between them have been extensively analysed by Astini et al. (2004). The studied sections corresponding to the Acoite Formation are exposed in Agua

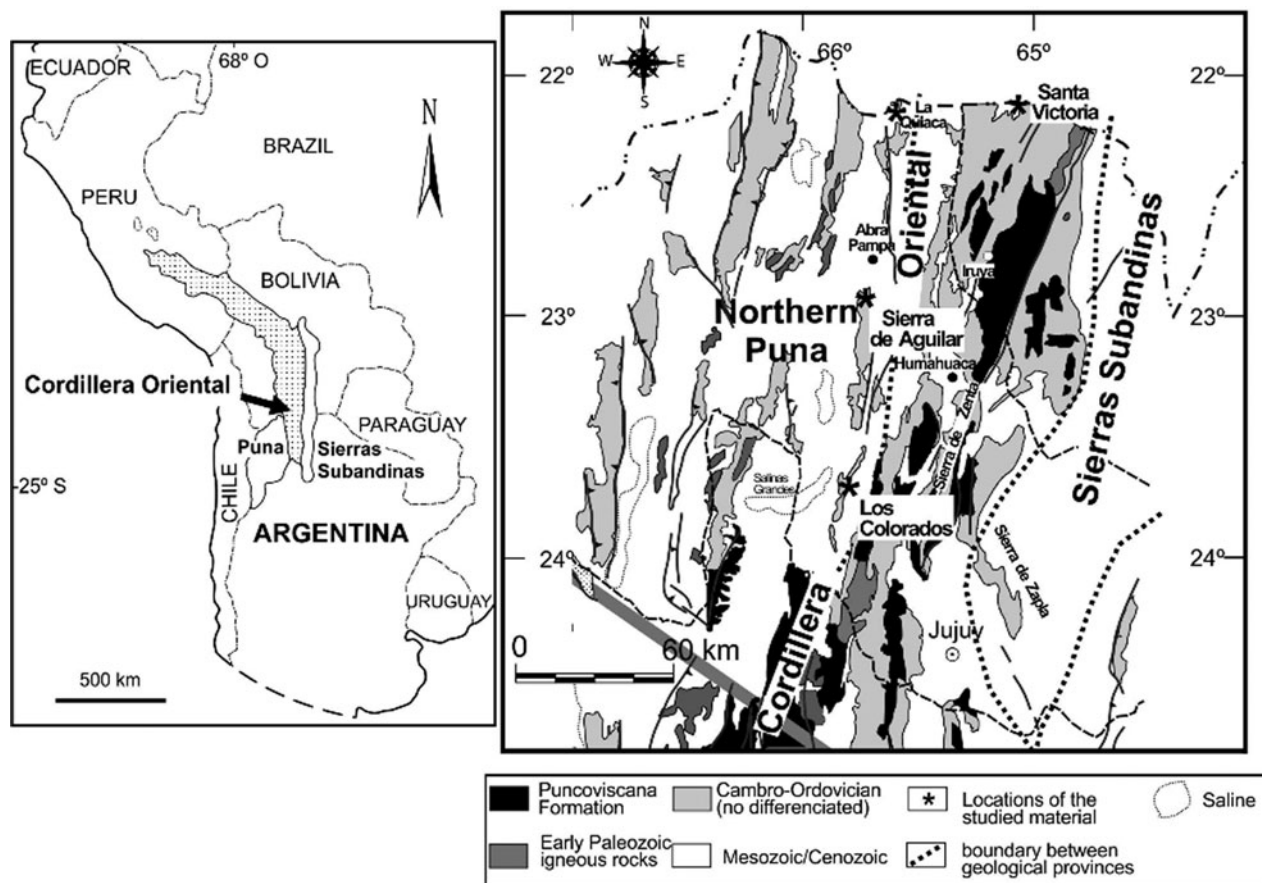


Figure 1. Map of the studied area.

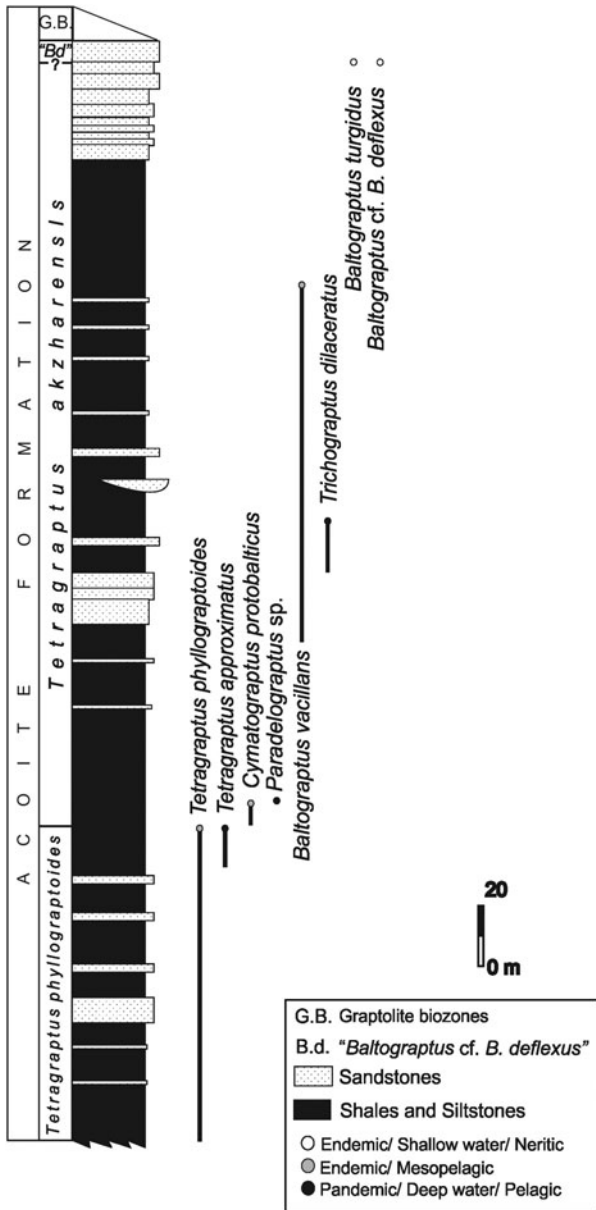


Figure 2. Combined stratigraphic column of Sierra de Aguilar area with distribution of the relevant taxa.

Blanca, Los Colorados and Chamarra creeks, and the integrated stratigraphic column is shown in Figure 2. The Acoite Formation reaches an approximate thickness of 3000 m in this area and has been the subject of numerous paleontological investigations (e.g. Astini and Waisfeld 1993; Toro 1997; Toro and Maletz 2008 and literature cited therein). The base of the unit is covered by modern deposits in Los Colorados Creek and affected by faulting at Agua Blanca Creek. The lower portion consists mainly of shales and greenish dark-grey silty shales, occasionally alternating with a few centimetre-thick sandstone levels and fine- to medium-grained and sterile carbonatic concretions with ‘cone-in-cone’ structures. These deposits have been

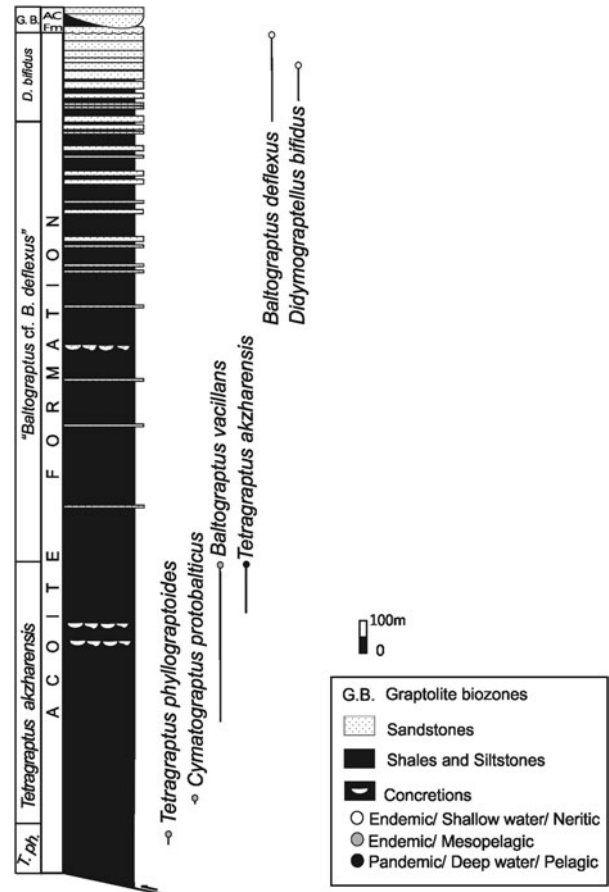


Figure 3. Combined stratigraphic column of Los Colorados area with distribution of the relevant taxa.

interpreted as belonging to an external platform. Similar pelitic levels integrate the lower portion of the Acoite Formation exposing in the northern end of the Sierra de Aguilar (Quinilicán, Agua Chica and Lumará creeks) (Figure 2). This area is located approximately 25 km to the south of the Abra Pampa village (Figure 1) and the studied succession presents a general Northwestern–Southeastern direction with an average thickness of approximately 600 m. A detailed discussion of the biostratigraphic aspects of the graptolites recorded in this area (*Tetragraptus phyllograptoides* and *Tetragraptus akzharensis* Zones) permitted recently to Toro and Vento (2013) to present an accurate correlation with the Los Colorados section.

The middle and upper portions of the Acoite Formation are clearly represented in the stratigraphic sections exposed in Los Colorados area (Los Colorados and Chamarra creeks). Greenish grey shales with rare interbedded sandstones alternate with bioturbated siltstones and heterolithic successions. They represent the transition from the outer to middle-inner shelf environments. Sandstone beds are progressively more abundant and more thickly bedded in the uppermost part of the unit,

corresponding to a shallower shore face environment, in which the *Didymograptellus bifidus* Zone is developed (Figure 3).

### Paleoecological considerations

The traditional patterns of spatial distribution of graptolites are based on the paleoenvironmental distribution and depth in the water column. However, both models are not independent and most recent works use both concepts to propose graptolite biofacies and biotopes (Egenhoff and Maletz 2007; Cooper et al. 2012) (Figure 3). Recently, Cooper et al. (2012) have reviewed the ecological model for planktonic graptolite habitats, considering three main groups of graptolites, according to their facies preference. A first group of species is confined to distal facies outer shelf, slope and ocean floor, corresponding to a dysaerobic facies, called 'pelagic biotope'. The second group can be located both in pelagic and neritic environments in the epipelagic biotope, and the third group is confined from inner to medium shelf neritic environments corresponding to the aerobic facies in the epipelagic zone (0–200 m). The last two groups mentioned by the authors were included in the 'neritic biofacies' to replace the previously known 'didymograptid biofacies' (Cooper et al. 1991; Mitchell et al. 2008) and 'endemic biofacies' fauna (Egenhoff and Maletz 2007). This includes most dichograptids, phyllograptids, some climacograptids, orthograptids, diplograptids, normalograptids, *Rhabdinopora* species and pendent didymograptids, as well as endemic species (Cooper et al. 2012), while the 'pelagic biofacies' has a greater diversity of faunas and includes most anisograptids, isograptids, sigmagraptids, nemagraptids and dicranograptids.

Toro (1994) recognised the didymograptid biofacies in north-western Argentina, due to the discovery of *D. bifidus*, *Phyllograptus* sp. and other pendent didymograptids. Later on, Toro (2002) briefly summarised the main results of that unpublished thesis, highlighting that this biotope was developed in the upper part of Acoite Formation, exposed in the Chamarra and Los Colorados creeks and corresponds to the deposits of the proximal portion of an internal platform with deltaic influence. Zhang et al. (2010) conducted an analysis of Ordovician graptolite diversity across several distinct lithofacies belts in South China, which represent nearshore, inner shelf, outer shelf, slope and basin environments. The investigation indicates that diversity increases progressively from nearshore towards the outer shelf, suggesting that the distribution of the analysed taxa was controlled mainly by water depth, basin morphology and distance from the coast.

However, one way to characterise an association of organisms consists in the identification and quantification of each species. Diversity data were obtained from the

revision of samples collected from the Sierra de Aguilar in the Cordillera Oriental. Using this information, we tried to represent them through a diversity diagram and to detect fluctuations in genus diversity for the early-middle Floian of north-western Argentina. The fossil record for the Floian is not complete in the study area since the preservation of the specimens is not optimal. Therefore, some interpretations about paleoecological analysis are limited for determining evolutionary schemes. The species composition changes along the space and time; a dominant species such as *Baltograptus geometricus* is replaced later by *B. vacillans*, this situation is coincident with the culmination of the lower biozone and the beginning of another biozone. Furthermore, the pattern of richness and abundance changes over the time, new species appear and others reduce their number until their extinction. It is also important to consider that in nature some species occur in a greater proportion and others are rare or scarce. Species such as *B. geometricus* and *B. vacillans* are abundant compared with other taxa such as *Paradelograptus* sp., which was found only once at Quinilicán Creek. The transition from one biozone to another would be related to the paleoenvironmental and paleoecological characteristics that would have effects on the decline or disappearance of species and the emergence and proliferation of other species in time (Vento 2013).

According to the distribution of the analysed characteristic taxa, presented in Figures 2 and 3, most of them are pandemic forms. It is important to highlight that this postulate is coincident with that observed by Toro (1994), whereas other species, such as *Baltograptus turgidus* and *Tetragraptus akzharensis*, are considered endemics although they have been recorded in more than one region in further studies, because they still have a very restricted distribution. However, the distribution of species in the Sierra de Aguilar allows to recognise deep water biofacies (Figure 3), corresponding to the external platform in the bottom part of the section, where the *Tetragraptus phyllograptoides* and *Tetragraptus akzharensis* biozones are developed (Vento 2013). This is supported by the presence of species such as *Cymatograptus protobalticus* that characterises the mesopelagic biotope (*sensu* Cooper et al. 1991) and corroborates the interpretation of Toro (1994) on the Acoite Formation exposed in Agua Blanca, Agua Chica and Lumará creeks.

Moreover, the presence of species of the *B. turgidus* group in fine- to middle-grained sandstones of the lower part of the '*Baltograptus* cf. *B. deflexus*' Zone, exposed in Quinilicán, Agua Chica and Lumará creeks, indicate the shallowing of this paleoenvironment, noting the transition to the inner shelf. Similar results have recently been presented by Zhang et al. (2010), the authors were based on the distribution of *B. turgidus* and the associated taxa, which are restricted to the shallow inner shelf in the Yangtze Region, south-western China. This information

together with the record of *B. turgidus* group, considered of endemic or highly restricted distribution, suggests the presence of a neritic biofacies (Figure 3) in the upper part of the studied sections of the Sierra de Aguilar area.

Finney and Berry (1997) suggested that the diversity and abundance of graptolites were higher in shallow waters, where phytoplankton production was higher and it descends into the deep ocean. However, the statistical analysis carried out by Zhang et al. (2010) suggests that the diversity from the Ordovician Period is low near the coast, but increases with water depth and the distance to shore, reaching a peak in the descending slope and back into the deep basin. The results obtained from the graph of Figure 4 are consistent with the last hypothesis.

During the Early-Middle Ordovician, graptolites underwent a rapid diversification. Many clades originated during this time, and this period was one of the most important in the evolutionary history of this fossil group (Zhang et al. 2007). The review of graptolites from Agua Chica and Lumará together with those from Quinilicán Creek permitted to develop a diversity scheme for the early-middle Floian, considering the total taxa identified in the Sierra de Aguilar area (Figure 4). The diversity of taxa in the Early-Middle Ordovician from the Sierra de Aguilar area shows an expansion from the 45 m, which could be due to an increase in the availability of resources such as light, nutrients, oxygen or others, which promoted the diversification of species in this environment. In the obtained curve, a number of fluctuations in relation to increments and decreases in the number of taxa present are highlighted, this situation may be due to the processes of emergence and extinction of species on a smaller scale.

The most spectacular event in the Early Ordovician was the rapid diversification of which evidence has been obtained from Baltica, Australasia and Avalonia (Cooper et al. 2004). Zhang et al. (2007) analysed the patterns of graptolite diversification in south-western China and compared their results with those coming from other regions. Their results show a significant diversity increase

during the early Floian, and they postulated that it could be due to differences in regional patterns of biodiversification in relation to the different paleoenvironments of each region. Achab and Paris (2007) conducted a study of chitinozoan biodiversification during the Ordovician, which suggests that it was progressive and showed similar patterns in Laurentia, Baltica and Gondwana.

The decrease in abundance and taxa richness observed and the record of endemic forms, or taxa of very restricted distribution, such as the *B. turgidus* group, are indicative of the shallowing of the upper part of the sequence studied in the Sierra de Aguilar. This is also consistent with the increasing particle size of sedimentary deposits and thickness of the sand bodies, which become more frequent in this part of the sequence. These observations could be extended to the Santa Victoria area, where the *B. turgidus* group is also present (Toro 1999; Vento 2013).

### Paleobiogeographic considerations

The analysis of the graptolites faunal affinities from north-western Argentina provides important information on understanding the paleogeographic relationship that existed between this region, located on the western margin of Gondwana, and the remaining paleocontinents in Lower Ordovician (Cocks and Torsvik 2002; Egenhoff and Maletz 2007). Despite the numerous studies conducted over the past years, including the study of the graptolites in the Cordillera Oriental, discussions of paleobiogeography are scarce and most of them are not supported by statistical analysis of the data.

Biostratigraphic and taxonomic knowledge of the fauna of Lower Ordovician graptolites has changed considerably, according to new data from around the world (Maletz 2005; Jackson and Lenz 2006; Zalasiewicz et al. 2009; Maletz and Ahlberg 2011). The paleogeographic implications derived from cluster analysis of new data from the Sierra de Aguilar and other areas of the Eastern Cordillera and Puna, compared with those fossils

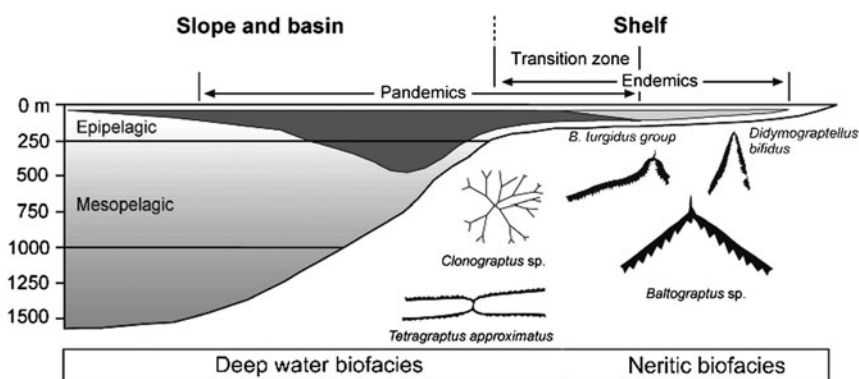


Figure 4. Graptolite biotopes and biofacies. Source: Modified from Egenhoff and Maletz (2007).

from Baltoscandia, Great Britain, south-western China and North America, are discussed in this section.

Traditionally, two faunal provinces have been recognised. First, the Atlantic Faunal Province or cold water realm is represented by Britain and Baltoscandia and it is characterised by a low diversity or low number of taxa. The Pacific Faunal Province or warm water realm is represented by North America and Australasia with a low diversity but high number of taxa (Finney and Chen 1990; Cooper et al. 1991). Also, various authors proposed the existence of a mixed region of faunas developed in middle latitudes. In Baltoscandia, taxa with Pacific faunal affinities were found with others restricted to the Atlantic domain, while in south-western China (Yangtze Region), Mu et al. (1979, 1980) and Chen (1994) indicated Atlantic affinities of the graptolite faunas. However, Chen (1994) proposed the hypothesis that some Pacific faunal taxa invaded the Atlantic Faunal Province during the early to middle Arenig (Floian).

The latitudinal thermal gradient of the surface waters is considered the basic primary control of graptolite provincialism but, in turn, it was controlled by the global climate of the earth, which was subject to change. The latitudinal thermal gradient of the surface water was also modified (as in modern oceans) by patterns of oceanic circulation. The influence of paleogeography on graptolite biogeography lies in the fact that the position of the continents affects the circulation patterns (Finney and Chen 1990).

The Baltoscandia and Yangtze Region situations are consistent with the paleogeographic location of the two regions in the mid-latitude transitional zone (Cooper et al. 1991). Mixed Atlantic and Pacific Faunal Province taxa associated with the pandemic forms were recognised in the deposits of Acoite Formation, north-western Argentina (Toro 1994, 1996). They can be found at levels assigned to the early Arenig (early to middle Floian) by the coexistence of tetragraptid forms traditionally considered indicators of Pacific affinities, such as *Tetragraptus akzharensis*, together with *Cymatograptus protobalticus* and *B. vacillans*, which are common in the Atlantic Faunal Province. In addition, the Pacific Faunal Province strongly influences the late Floian levels of the studied sequence too, as *D. bifidus* is associated with elements of Atlantic faunal affinities as *Baltograptus minutus* and *B. deflexus*. Furthermore, the presence of forms that previously had been reported only from the Yangtze Region of China, as *B. turgidus* and *B. kunmingensis*, and many common species reported in Baltoscandia, as *Trichograptus dilaceratus*, *Corymbograptus v-fractus tullbergi* and *Expansograptus latus*, are also significant. This suggests a close relationship between graptolites from north-western Argentina and those of the two mentioned regions, which have been of mixed origin and located in the

transition zone of mid-latitudes, as was postulated by Toro (1994, 1996).

The close paleogeographic relationship of the Cordillera Oriental, Argentina, with Baltica was initially highlighted by Toro (1993, 1994). This relationship was based mainly on the presence of declined and deflexed didymograptids, primarily of the genera *Baltograptus* and *Cymatograptus*. Subsequently, studies reaffirmed the affinities with the cold water Atlantic Faunal Province, and especially with Baltoscandian faunas (Maletz and Ortega 1995; Toro and Maletz 2007). More recently, Vento et al. (2012) have conducted a detail statistical analysis to evaluate new records of the early Floian taxa from north-western Argentina, which clearly corroborate the strong relationships between both regions.

The significant affinity between graptolite from the '*Baltograptus* cf. *B. deflexus*' and *D. bifidus* Zones of the Eastern Cordillera and the Yangtze Province (south-western China) was first established by Toro (1994, 1996). New paleontological data from other parts of the world were considered in this study, in order to obtain more information about the paleobiogeographic relations of north-western Argentina during the Floian. Our data were compared with equivalent records recently provided for Baltoscandia (Egenhoff and Maletz 2007), Great Britain (Zalasiewicz et al. 2009), North America (Williams and Stevens 1988; Jackson and Lenz 2006) and south-western China (Zhang et al. 2007, 2010), using a cluster analysis that quantifies paleogeographic relations between these regions.

A presence-absence matrix including all taxa registered in the equivalent biozones to the '*Baltograptus* cf. *B. deflexus*' and *D. bifidus* Biozones was developed to obtain a more detailed graphic of the variation of faunal affinities across that range (the presence-absence matrix available upon request). The matrix included Floian species previously recognised from the Sierra de Aguilar (Toro 1994, 1996, 1997). It also incorporated other graptolite records from the late Floian mentioned and described for north-western Argentina (Toro and Brussa 2003; Albanesi et al. 2008).

The cluster analysis presented in Figure 6 was carried out using the statistical program Past and the Jaccard index was used for measuring biodiversity. Taxa from the '*Baltograptus* cf. *B. deflexus*' and *D. bifidus* Biozones for the middle and late Floian were considered. The dendrogram shows moderate affinities between north-western Argentina and south-western China, with a Jaccard index of 0.45. Also, a clustering between Baltoscandia and Britain by an index of about 0.60 is observed. In turn, this grouping has an index close to 0.40 considering north-western Argentina, and a lower affinity with the south-western region of China during the middle-late Floian. North America is separated from the other regions with a value of 0.25, showing the low affinity with the north-western Argentina faunas.

It is worth pointing out that the results of this study constitute the necessary complement to the previous paleobiogeographical attempts, and rely on the records of *Trichograptus dilaceratus*, *Acrograptus gracilis*, *E. latus* and *Corymbograptus v-fractus tullbergi*, which were found for the first time in Argentina by Vento and Toro (2009) and Vento et al. (2010, 2012). *Trichograptus dilaceratus* is restricted to grey and green shales of the lower levels of the Acoite Formation, which would indicate deep water facies. Cooper et al. (1991) and Egenhoff and Maletz (2007) identified this species as an element of deep sea fauna pandemic, which has not been recognised so far in any region of the Pacific Faunal Province. Instead, the *B. turgidus* group is located in fine-grained sandstones medium corresponding to shallow water facies. Zhang et al. (2010) have recently considered that the *Baltograptus varicosus* group (related to the *B. turgidus* group of China) is ecologically restricted to the shallow water biofacies. Therefore, the distribution of *Trichograptus dilaceratus* and the *B. turgidus* group species in north-western Argentina is consistent with the above considerations, regarding the importance of these taxa as paleoenvironmental indicators.

The statistical analysis confirms the previous paleobiogeographic relations observed in other areas of the Cordillera Oriental (Toro 1994, 1996), it supports the hypothesis that during the Early Ordovician, north-western Argentina, as part of the supercontinent Gondwana, was located in middle to high latitudes or the cold water faunal realm (Atlantic Faunal Province) (Maletz and Ortega 1995; Toro and Maletz 2007).

Similar Floian graptolite faunas with *Baltograptus* and *Cymatograptus* species were found in Baltica, Avalonia

and south-western China, but not in North America. Moreover, the strong paleogeographic relations between north-western Argentina and Baltoscandia during the early Floian (Vento et al. 2012) become more significant with south-western China during the middle and late Floian (Figure 5). This can be explained by the paleoenvironmental influence that is related to the platform gradient, which determined the development of deep water biofacies in the north-western Argentina and Baltoscandia (*Tetragraptus phyllograptoides* and *Tetragraptus akzharensis* Zones) and neritic biofacies in north-western Argentina and south-western China ('*Baltograptus* cf. *B. deflexus*' and *D. bifidus* Zones). The influence of paleoenvironmental factors related to shallowing events that are reflected in the development of biofacies recognised in the Acoite Formation deposits was suggested earlier by Toro (1994) and remains in Vento (2013). This influence overlaps the latitudinal gradient to explain the coexistence of forms with affinities of the Atlantic and Pacific Faunal Provinces of graptolites in the *D. bifidus* Zone and other endemic or geographically restricted forms such as *B. turgidus* in the lower part of the '*Baltograptus* cf. *B. deflexus*' Zone.

Moreover, the associations of chitinozoans and marine phytoplankton also suggest a high to intermediate paleolatitudinal position for Early Ordovician (de la Puente and Rubinstein 2012). The acritarchs in Tremadocian–Floian interval indicates a close relationship of this region with the peri-Gondwanan domain characterised by containing cold to warm water elements (Rubinstein et al. 2007). Chitinozoan associations of upper early Floian and lower middle Floian for the eastern part of the Cordillera Oriental have affinities with northern Gondwana and the

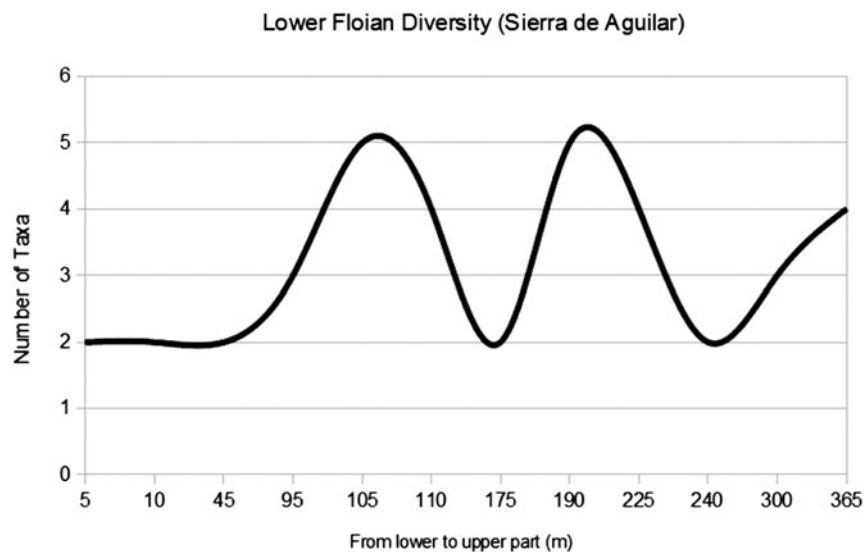


Figure 5. Taxa variation along the stratigraphic section (Sierra de Aguilar).



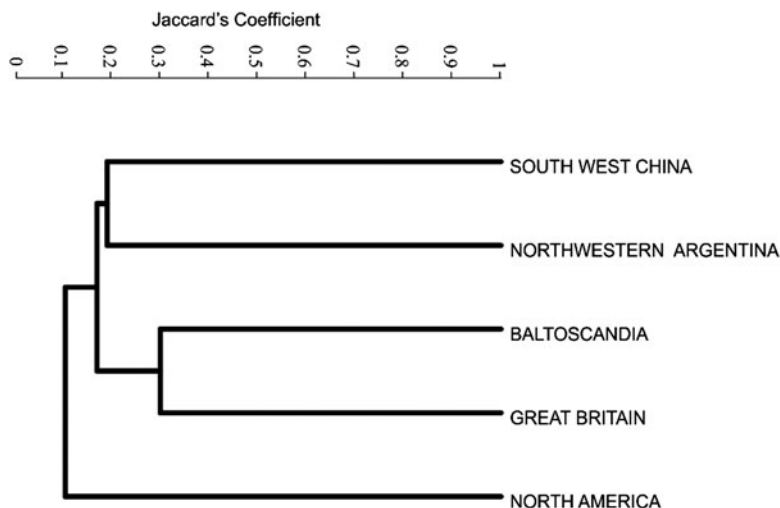


Figure 6. Cluster showing the faunistic affinities (using Past software).

South China plate. The chitinozoans of this area show a cosmopolitan character in the late Floian, which is already evident from the upper middle Floian in the western section of the Eastern Cordillera associations. This would be possibly due to a pulse in early ocean circulation thermohaline activation that took place during the Middle Ordovician at a global scale (de la Puente 2010). The intermediate latitudinal position has been suggested as the main cause of the taxon mixture from different paleobiogeographic provinces of other fossil groups as trilobites and brachiopods of Early Ordovician of north-western Argentina (Benedetto et al. 2009).

### Conclusions

According to the distribution of Floian graptolites from north-western Argentina, the presence of three different biofacies in sedimentary deposits of the Acoite Formation is recognised. The first deep water biofacies is developed in pelitic levels, which constitute the lower part of the unit (*Tetraraptus phyllograptoides* and *Tetraraptus akzharensis* Zones). It is represented by pandemic forms, such as *Tetraraptus approximatus*, together with mesopelagic forms, such as *Cymatograptus protobalticus*. The other two biofacies belong to the endemic or neritic shallow environments. They are developed in the upper deposits of the lower half of the Acoite Formation (bottom of *Baltograptus* cf. *B. deflexus* Zone), in the Sierra de Aguilar, and in the upper portion of the unit exposed in Los Colorados area (*D. bifidus* Zone), respectively.

Paleogeographic relationships between the north-western Argentina and south-western China during the middle and late Floian can be explained by the paleoenvironmental influence that is related to the platform gradient, which determined the development of deep

water biofacies in north-western Argentina and Baltoscandia (*Tetraraptus phyllograptoides* and *Tetraraptus akzharensis* Zones) and neritic biofacies in north-western Argentina and south-western China (*Baltograptus* cf. *B. deflexus*' and *D. bifidus* Zones).

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### Notes

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### References

- Achab A, Paris F. 2007. The Ordovician chitinozoan biodiversification and its leading factors. *Palaeogeogr Palaeoclimatol Paleoecol.* 245:5–19.
- Albanesi G, Ortega G, Zeballos F. 2008. Faunas de conodontes y graptolitos del paleozoico inferior en la Cordillera Oriental Argentina. *Relatorio del XVII Congreso Geológico Argentino.* Jujuy. p. 98–118.
- Astini RA. 2003. The Ordovician Proto-Andean basins. In: Benedetto JL, editor. *Ordovician fossils of Argentina.* Secretaría de Ciencias y Tecnología, Universidad Nacional de Córdoba, Córdoba. p. 1–74.
- Astini RA. 2008. Sedimentación, facies, discordancias y evolución paleoambiental durante el Cambro-Ordovícico. *Relatorio del XVII Congreso Geológico Argentino.* Jujuy. p. 50–73.
- Astini RA, Waisfeld BG. 1993. Análisis estratigráfico y paleoambiental del Ordovícico inferior (Formaciones Acoite y Sepulturas) al Oeste de Purmamarca, Cordillera Oriental jujeña. *XII Congreso Geológico Argentino y II Congreso de Exploración de Hidrocarburos.* Mendoza. 1. p. 96–106.
- Astini RA, Waisfeld BG, Toro BA, Benedetto JL. 2004. El Paleozoico inferior y medio de la región de Los Colorados, borde occidental de la Cordillera Oriental (provincia de Jujuy). *RAGA.* 59(2):243–260.

- Bahlburg H, Furlong KP. 1996. Lithospheric modeling of the Ordovician foreland basin in the Puna, NW Argentina: on the influence of arc loading on foreland basin formation. *Tectonophysics*. 259:245–258.
- Benedetto JL, Vaccari NE, Waisfeld BE, Sánchez TM, Foglia RD. 2009. Cambrian and Ordovician biogeography of the South American margin of Gondwana and accreted terranes. *Geol Soc Lond Spec Publ*. 325:201–232.
- Berry WBN. 1962. Graptolite occurrence and ecology. *J Paleontol*. 36:285–293.
- Berry WBN. 1974. Types of Early Paleozoic faunal replacements in North America: their relationship to environmental change. *J Geol*. 82:371–382.
- Bulman O. 1964. Lower Palaeozoic plankton. *Quart J Geol Soc*. 120:455–476.
- Bulman OMB. 1971. Graptolite faunal distribution. In: Middlemiss FA, Rawson PF, Newell G, editors. *Faunal provinces in space and time*. *Geol J Spec* 4:47–60.
- Bulman OMB. 1978. On the geographical distribution of graptolites. *Recent Res Geol*. 5:90–95.
- Chen X. 1994. Arenig to Llanvirn graptolite provincialism. In: Chen X, Erdtmann BD, Ni YN, editors. *Graptolite research today*. Nanjing: Nanjing University Press. p. 223–239.
- Cocks LMR, Torsvik TH. 2002. Earth geography from 500 to 400 million years ago: a faunal and palaeomagnetic review. *J Geol Soc*. 159:631–644.
- Cooper RA. 1998. Towards a general model for the depth ecology of graptolites. In: Gutiérrez-Marco JC, Rábano I, editors. *Proceedings of the VI international graptolite conference (GWG-IPA)*. España: Instituto Geominero de España. p. 161–163.
- Cooper RA, Fortey RA, Lindholm K. 1991. Latitudinal and depth zonation of Early Ordovician graptolites. *Lethaia*. 24:199–218.
- Cooper RA, Maletz J, Taylor L, Zalasiewicz JA. 2004. Graptolites: patterns of diversity across paleolatitudes. In: Webby BD, Paris F, Droser ML, Percival IG, editors. *The Great Ordovician biodiversification event*. New York, NY: Columbia University Press. p. 281–293.
- Cooper RA, Rigby S, Loydell DK, Bates DEB. 2012. Palaeoecology of the Graptoloidea. *Earth Sci Rev*. 112(2012):23–41.
- de la Puente GS. 2010. Quitinozoos del Floiano (Ordovícico Inferior) del área de Santa Victoria, Cordillera Oriental, noroeste argentino. Parte 2: Implicancias bioestratigráficas, paleobiogeográficas y paleoambientales. *Ameghiniana*. 47:317–330.
- de la Puente GS, Rubinstein CV. 2012. Ordovician chitinozoans and marine phytoplankton of the Central Andean Basin, northwestern Argentina: a biostratigraphic and paleobiogeographic approach. *Rev Palaeobot Palynol*. doi:10.1016/j.revpalbo.2012.03.007
- Egenhoff S, Maletz J. 2007. Graptolites as indicators of maximum flooding surfaces in monotonous deep-water shelf sequences. *Palaios*. 22:373–383.
- Erdtmann BD. 1976. Ecostratigraphy of Ordovician graptoloids. In: Bassett MG, editor. *The Ordovician system*. Cardiff: University of Wales Press and National Museum of Wales. p. 621–643.
- Erdtmann BD. 1984. Outline ecostratigraphic analysis of the Ordovician graptolite zones in Scandinavia in relation to the palaeogeographic disposition of the Iapetus. *Geol Palaentol*. 18:9–15.
- Finney SC, Berry WBN. 1997. New perspectives on graptolite distributions and their use as indicators of platform margin dynamics. *Geology*. 25(10):919–922.
- Finney SC, Chen X. 1990. The relationship of Ordovician graptolite provincialism to palaeogeography. *Geol Soc Lond Mem*. 12:123–128.
- Jackson DE, Lenz AC. 2006. The sequence and correlation of Early Ordovician (Arenig) graptolite faunas in the Richardson trough and Misty creek Embayment, Yukon territory and District of Mackenzie, Canada. *Can J Earth Sci*. 43:1791–1820.
- Maletz J. 2005. Early Middle Ordovician graptolite biostratigraphy of the Lovisefred and Albjära drill cores (Scania, southern Sweden). *Palaeontology*. 48:763–780.
- Maletz J, Ahlberg P. 2011. The Lerhamn drill core and its bearing for the graptolite biostratigraphy of the Ordovician Tøyen Shale in Scania, southern Sweden. *Lethaia*. 44(3):350–368.
- Maletz J, Ortega G. 1995. Ordovician graptolites of South America: palaeogeographic implications. In: Cooper JD, Droser JD, Finney SC, editors. *Ordovician Odyssey: short papers for the seventh international symposium on the Ordovician system*. Fullerton, CA: Pacific Section Society for Sedimentary Geology (SEPM). p. 189–192.
- Mitchell CE, Brussa ED, Maletz J. 2008. A mixed isograptid-didymograptid graptolite assemblage from the Middle Ordovician of west Gondwana (NW Bolivia): implications for graptolite paleoecology. *J Paleontol*. 82(6):1114–1126.
- Mu EZ, Ge MY, Chen X, Ni YN, Lin YK. 1979. Lower Ordovician graptolites of Southwest China. *Palaeontol Sin New Ser B*. 156:1–192.
- Mu EZ, Li JJ, Ge MY, Chen X, Ni YN, Lin YK. 1980. Ordovician graptolite sequence and biogeographic regions in China. *Scientific papers on geology for international exchange, stratigraphy and palaeontology*. Beijing: Publishing House of Geology. p. 35–42.
- Raymont JEG. 1983. *Plankton and productivity in the oceans*. Vol. 2 *Zooplankton*. New York, NY: Pergamon Press.
- Ross RJ, Jr. 1961. Distribution of Ordovician graptolites in eugeosynclinal facies in western North America and its paleogeographic implications. *Am Assoc Petrol Geol Bull*. 45:330–341.
- Rubinstein CV, de la Puente GS, Toro BA, Servais T. 2007. The presence of the messaoudensis-trifidum acritarch assemblage (Upper Tremadocian-Floian) in the Central Andean Basin, north-western Argentina: calibration with chitinozoans and graptolite zonation. 10th International symposium on the Ordovician system, Nanjing, China. *Acta Palaeontol Sin* 46:422–428.
- Skevington D. 1973. Ordovician graptolites. In: Hallam A, editor. *Atlas of palaeobiogeography*. Amsterdam, NY, USA: Elsevier Scientific Publishing Company. p. 27–35.
- Skevington D. 1974. Controls influencing the composition and distribution of Ordovician graptolite faunal provinces. *Spec Pap Palaeontol*. 13:58–73.
- Skevington DA. 1976. A discussion of the factors responsible for the provincialism displayed by graptolite faunas during the Early Ordovician. In: Kaljo D, Koren, T, editors. *Graptolites and stratigraphy*. Tallinn: Academy of Sciences of Estonian SSR, Institute of Geology. p. 180–201.
- Toro BA. 1993. Graptofauna arenigiana de la quebrada del río Cajas (Formación Acoite), provincia de Jujuy, Argentina. *Ameghiniana*. 30(1):69–76.
- Toro BA. 1994. Taxonomía, bioestratigrafía y afinidades paleobiogeográficas en base a las graptofaunas ordovícicas del borde occidental de la Cordillera Oriental, provincia de Jujuy, Argentina [tesis doctoral]. Córdoba. Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba. 173 p. (Inédito).
- Toro BA. 1996. Implicancias paleobiogeográficas del hallazgo de *Baltograptus turgidus* (Lee) y *Baltograptus kunningensis* (Ni) (Graptolithina) en el Arenigiano Temprano del Noroeste de Argentina. XIII Congreso Geológico Argentino y III Congreso de Exploración de Hidrocarburos. *Actas*. 5:27–38.
- Toro BA. 1997. La fauna de graptolitos de la Formación Acoite, en el borde occidental de la Cordillera Oriental Argentina. *Análisis bioestratigráfico*. *Ameghiniana*. 34(4):393–412.
- Toro BA. 1999. Nuevos datos paleontológicos (Graptolithina), bioestratigráficos y paleogeográficos del área de Santa Victoria, Cordillera Oriental, Argentina. *Ameghiniana*. 36:477–487.
- Toro BA. 2002. Biostratigraphic and paleobiogeographic analysis of the graptolites from the Lower Paleozoic of the Cordillera Oriental, Argentina. Tromboto DT, Villalba R, editors. *IANIGLA, 30 years of basic and applied research on environmental sciences*. Mendoza, Argentina. p. 182–193.
- Toro BA, Brussa ED. 2003. Graptolites. In: Benedetto JL, editor. *Ordovician fossils of Argentina*. Secretaría de Ciencia y Tecnología, Universidad Nacional de Córdoba, Córdoba. p. 441–505.
- Toro BA, Maletz J. 2007. Deflexed *Baltograptus* species in the early to mid Arenig graptolite biostratigraphy of Northwestern Argentina. *Acta Palaeontol Sin*. 46:489–498.
- Toro BA, Maletz J. 2008. The proximal development in *Cymatograptus* (Graptoloidea) from Argentina and its relevance for the early evolution of Dichograptacea. *J Paleontol*. 85(5):974–983.
- Toro BA, Vento BA. 2013. Reevaluación de las biozonas de Tetragraptus phyllograptoides y Tetragraptus akzharensis (Ordovícico inferior,

- Floiano) de la Cordillera Oriental Argentina. *Ameghiniana*. 50 (3):287–297.
- Vento BA. 2013. Cuantificación de las relaciones taxonómicas, filogenéticas y de los patrones paleoecológicos de los graptolitos del Paleozoico inferior del noroeste de Argentina [tesis doctoral]. Mendoza, Argentina. Facultad de Ciencias Medicas, Universidad Nacional de Cuyo, 332 p. (Inédito).
- Vento B, Toro B. 2009. Resultados preliminares del estudio taxonómico de los graptolitos del Paleozoico inferior del Noroeste de Argentina. *Ameghiniana*, Suplemento, Resúmenes. 46(4):95–96.
- Vento B, Toro B, Maletz J. 2010. New insights for the paleobiogeographic analysis of the early Ordovician graptolite fauna of northwestern Argentina. X Congreso Argentino de Paleontología y Biostratigrafía y VII Congreso Latinoamericano de Paleontología Resúmenes. Museo de La Plata. La Plata. p. 56–57.
- Vento B, Toro BA, Maletz J. 2012. New insights into the paleobiogeography of the early Ordovician graptolite fauna of northwestern Argentina. *Comptes Rendus Palevol*. 11(5):345–355.
- Waisfeld B. 1993. Concentraciones fosilíferas autóctonas y para-autóctonas en la Formación Acoite (Ordovícico Temprano), Cordillera Oriental, Provincia de Jujuy. Consideraciones tafonómicas y paleoecológicas. In: IAPG, editor. XII Congreso Geológico Argentino y II Congreso de Exploración de Hidrocarburos. Actas, Tomo II. p. 296–303.
- Webby BD, Paris F, Droser ML, Percival IG, editors. 2004. The Great Ordovician biodiversification event. New York, NY: Columbia University Press, 484 p.
- Williams A. 1969. Ordovician faunal provinces with reference to brachiopod distribution. In: Wood A, editor. The Precambrian and Lower Palaeozoic rocks of wales. Cardiff: University of Wales Press. p. 117–154.
- Williams SH, Stevens RK. 1988. Early Ordovician (Arenig) graptolites of the Cow Head Group, western Newfoundland, Canada. Vol. 5. *Palaeontographica Canadiana*. Toronto: University of Toronto Press. 167 p.
- Zalasiewicz JA, Taylor L, Rushton AWA, Loydell DK, Rickards RB, Williams M. 2009. Graptolites in British stratigraphy. *Geol Mag*. 146 (6):785–850.
- Zhang YD, Chen X, Goldman D. 2007. Diversification patterns of Early and Mid Ordovician graptolites in South China. *Geol J*. 42(3–4):315–337.
- Zhang YD, Chen X, Goldman D, Zhang J, Cheng J, Song Y. 2010. Diversity and paleobiogeographic distribution patterns of Early and Middle Ordovician graptolites in distinct depositional environments of South China. *Sci China Earth Sci*. 53:1811–1827.