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The brachiopod *Kvania*, a biostratigraphic marker across the Cambrian-Ordovician boundary in Andean Gondwana

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ABSTRACT. The plectorthoid brachiopod *Kvania* is widely distributed in Upper Cambrian and Lower Ordovician rocks of the Central Andean basin of northwestern Argentina and southwestern Bolivia. In this contribution, *Kvania lariensis* Benedetto is reported for the first time in the Eastern Cordillera (Quebrada de Humahuaca area) of northwestern Argentina. Studied material comes from the Alfarcito Member of the Santa Rosita Formation (Santa Victoria Group) of well constrained earliest Tremadocian age (Tr1). The presence of *Kvania lariensis* in different localities of the Altiplano-Puna region and the Eastern Cordillera of Bolivia and Argentina allows proposing this species as a reliable biostratigraphic marker for the lowermost Ordovician of the region. On the basis of the phylogenetic hypothesis supporting the *Protorthisina-Kvania-Gondwanorthis* lineage, four phylozones are recognized across the Cambrian-Ordovician boundary. The basal member of the lineage is *Kvania primigenia*, which co-occurs with *Parabolina* (*Neoparabolina*) *frequens argentina*, is proposed here as a biostratigraphic marker for the upper Furongian (Stage 10). The base of the time slice Tr1 is indicated by the first appearance of *Kvania lariensis*, which is almost time-equivalent to the *Jujuyaspis keideli* trilobite biozone, whereas the descendent species *Kvania azulpampensis* is almost coeval with the *Kainella andina* trilobite biozone. *Gondwanorthis calderensis calderensis*, a more derived member of the lineage, indicates the upper part of the lower Tremadocian (Tr1), and is equivalent to the *Kainella meridionalis* trilobite biozone. The specimens of *Kvania lariensis* from the Alfarcito Member provide additional information about its phenotypic variablity, confirming the trend of increasing costellae number through ontogeny observed in the type material, and also corroborate that the lineage as a whole experienced a defined evolutionary trend to increasing both shell size and costellae number.

Keywords: Phylozones, Biostratigraphy, Brachiopods, Furongian, Tremadocian, NW Argentina, Central Andean basin.

RESUMEN. El braquiópodo *Kvania*, un marcador bioestratigráfico a través del límite Cámbrico-Ordovícico en la región Andina de Gondwana. El braquiópodo plectortoideo *Kvania* está ampliamente distribuido en el Cámbrico Superior y Ordovícico Inferior de la cuenca Andina Central del noroeste de Argentina y suroeste de Bolivia. En esta contribución, la especie *Kvania lariensis* Benedetto es reportada por primera vez en el área de la quebrada de Humahuaca de la cordillera Oriental del noroeste argentino. El material estudiado proviene del Miembro Alfarcito de la Formación Santa Rosita (Grupo Santa Victoria) del Tremadociano temprano (Tr1). *Kvania lariensis* está presente en diferentes localidades del altiplano-puna y de la cordillera Oriental de Bolivia y Argentina, por lo que se propone a esta especie como un marcador bioestratigráfico para el Ordovícico más temprano de la cuenca Andina Central. Sobre la base de la hipótesis filogenética del linaje *Protorthisina-Kvania-Gondwanorthis*, se reconoce un esquema cuadripartito de filozonas a través del límite Cámbrico-Ordovícico. *Kvania primigenia*, el miembro basal del linaje, ocurre simultáneamente con *Parabolina* (*Neoparabolina*) *frequens argentina* en difentes localidades, por lo que es propuesto aquí como marcador bioestratigráfico para el Furongiano Superior (Piso 10). La base del Tremadociano Inferior (intervalo Tr1) es indicada por la primera aparición de *Kvania lariensis*, la cual es aproximadamente equivalente en edad a la biozona de *Jujuyaspis keideli*, mientras que la especie descendiente *Kvania azulpampensis* lo es respecto de la biozona de *Kainella andina. Gondwanorthis calderensis calderensis*, la subespecie más derivada del lineaje, indica la parte superior del Tremadociano Inferior (Tr1) y es equivalente a la biozona de *Kainella meridionalis*. Los especímenes de *Kvania lariensis* colectados en el Miembro Alfarcito proveen información adicional sobre su variabilidad fenotípica y confirman la tendencia al incremento del número de costillas durante la ontogenia de la especie. También se corrobora que el linaje en su conjunto experimentó un definida tendencia evolutiva hacia el incremento del tamaño de las valvas y del número total de costillas.

Palabras clave: Filozonas, Bioestratigrafía, Braquiópodos, Furongiano, Tremadociano, Noroeste de Argentina, Cuenca Andina Central.

1. Introduction

Paleozoic brachiopods have been rarely used as biostratigraphic markers because of their benthic lifestyle and their preference for shallow water settings. These environments are generally unfavourable for traditional markers such as graptolites and conodonts, but in the absence of such fossils, brachiopods can be potentially useful to establish a chronology (*e.g.*, Ziegler, 1966; Baarli and Johnson, 1988; Laurie, 1991; Jin, 2001; Reyes-Abril *et al.*, 2011; Sohrabi and Jin, 2013), as well as for locating systemic boundaries (*e.g.*, Mottequin *et al.*, 2014; Angiolini *et al.*, 2021).

The first brachiopod-based biostratigraphic scheme for southwestern Gondwana was proposed by Herrera and Benedetto (1991), who erected five "assemblage" biozones through the Tremadocian-Darriwilian carbonate succession of the Precordillera basin of western Argentina. These biozones proved to be useful for intrabasinal correlations and, to a lesser extent, for correlations with neighboring (*e.g.*, Famatina) basins. They were further redefined as "taxon-range" biozones and their taxonomic composition was updated (Benedetto, 2002). Although the set of taxa recorded in each biozone reflects primarily the evolution of brachiopod lineages through time, it is also conditioned by the environmental changes that took place in the basin, as well as by the relative paleogeographic placement of the far-travelled Precordillera terrane through time (Benedetto, 1998a, 2007a; Benedetto *et al.*, 1999). The sum of these biologic, climatic and tectonic factors allowed each taxon-range biozone to experience some taxonomic variability and often some degree of diachronism through the basin.

A rather different biostratigraphic scheme based on "lineage biozones" or "phylozones" was proposed later for the Furongian-Lower Ordovician successions of northwestern Argentina (Benedetto, 2005). A lineage biozone, according to the definition of the North American Stratigraphic Code (2005, p. 1574) is "...a body of rock containing species representing a specific segment of an evolutionary lineage". The successive taxa forming the evolutionary lineage constitute a powerful tool to establish biostratigraphic schemes, in particular in those cases where morphological changes along the lineage concentrate in short periods of time, and the new evolved species remain nearly unchanged (morphological stasis) until the next speciation event. Most lineages usually split in two, originating new species in the process of cladogenesis. In the example posed here, coexistence in the same stratigraphic horizon of ancestral and descendent species has not been observed, so that the simplest scenario is one in which a single lineage punctuated by phenotypic changes (punctuated anagenesis; see Jackson and Cheetham, 1999) spreads throughout the basin. However, the fact that closely allied species of *Kvania* are present in upper Tremadocian rocks of central Europe (*e.g.*, Havlíček, 1994; Szduy *et al.*, 2001), coexisting with or postdating the more derived members of the Andean lineage (*e.g.*, *Gondwanorthis* and *Lampazarorthis*), strongly suggests the occurrence of one or more cladogenetic events in the region, as the cladistic analysis of plectorthoids performed by Benedetto and Muñoz (2017) demonstrated. On the other hand, there is no conclusive evidence of the so-called "punctuated gradualism", in which a lineage shows both punctuation and gradual change (Fortey, 1988) since no morphological transition between ancestral and descendent species has been observed in the lineage under consideration. However, since distinction of the terms "gradual" and "rapid" when applied to morphologic evolution in the fossil record is ambiguous and has been subject to varying interpretations by different authors, an explicit, statistical analysis is necessary to comprehensively define the evolutionary pattern (Hunt, 2008).

The time interval covered by the successive species of a lineage can vary somewhat, but it can be usually as short as the conodont or graptolite biozones. A further advantage of phylozones is that, due to the nature of evolutionary process, there should be no significant overlap in the ranges of ancestral and descendent species along the lineage. However, this is not always the case, being true only in those lineages showing an anagenetic (punctuated or gradual) pattern. For instance, in the Upper Ordovician of Laurentia, the older and smaller species of *Zygospira* co-existed with younger species that evolved throughout the Katian, which is interpreted as a case of sympatric speciation where a single ancestral species gave rise to new species probably by niche partitioning (Sproat and McLeod, 2023). In the *Kvania* example from above, nevertheless, there is no evidence that *Kvania lariensis* coexisted neither with the ancestral species *K. primigenia* nor with the descendent *K. azulpampensis*, although further research at the basin scale is needed to fully clarify the evolutionary pattern.

As in other biostratigraphic units, in the phylozones the boundaries are surfaces that mark the lowest (first appearance datum; FAD) and highest (last appeareance datum; LAD) occurrence of successive taxa along the evolutionary lineage. Whenever the lowest appearance of successive segments in a lineage over the area of their distribution can be considered as basically synchronous, the lineage zones allow precise correlations to be established (Tanaka and Takahasi, 2013). In the practice, however, identification of such evolutionary lineages is not always possible since it requires of a nearly uninterrupted stratigraphic succession lacking abrupt environmental shifts and, most importantly, an essentially continuous series of phylogenetically linked taxa. In northwestern Argentina, the ~3,500 m-thick platform and shoreface clastic successions of the Santa Victoria Group (Waisfeld *et al.*, 2023, and references therein) constitutes an excellent case study since rhynchonelliform brachiopods of Late Cambrian to late Floian age are abundant in there and well preserved throughout the unit (Benedetto, 1998b, 2007b; Benedetto and Carrasco, 2002; Harper *et al.*, 2004; Villas and Herrera, 2004; Villas *et al.*, 2009; Muñoz and Benedetto, 2016; Benedetto and Muñoz, 2017). Also interesting is that fossiliferous levels often include more or less continuous series of early juvenile to gerontic individuals, allowing to reconstruct the ontogenetic trajectories of some species and hence to infer morphological trends directed by heterochronic processes (Benedetto, 2007b).

In this contribution, *Kvania lariensis* Benedetto is reported for the first time from the Eastern Cordillera of the Jujuy Province, from beds of well constrained earliest Tremadocian age (Tr1). The species *K. lariensis* is a basal form within the Furongian-Early Ordovician *Protorthisina-Kvania-Gondwanorthis-Lampazarorthis-Tarfaya* plectorthoid lineage (Benedetto and Muñoz, 2017). The presence of *K. lariensis* in widely separated localities of the Altiplano-Puna region and the Eastern Cordillera of Bolivia and northwestern Argentina, along with its well-constrained conodont and graptolite-based age, leaves this species as a useful biostratigraphic marker for the lowermost Ordovician of the Central Andean basin of Gondwana. Moreover, other taxa of this phylogenetic lineage, in particular the descending species *Kvania azulpampensis* and *Gondwanorthis calderensis calderensis* also constitute regional index fossils. The purpose of this contribution is therefore to review and update available chronostratigraphic information since the first attempt of a brachiopod-based biozonation for the Ordovician of the Central Andean basin (Benedetto, 2005), and also to propose the species *K. primigenia* as a reliable biostratigraphic marker for the upper Furongian. Finally, equivalences among the brachiopod-based and the trilobite-based biostratigraphic schemes are examined.

2. Geological setting

Lower Paleozoic rocks in northwestern Argentina and southwestern Bolivia are superbly exposed in the vast Central Andean basin encompassing the Eastern Cordillera and the Subandean Ranges (*e.g.*, Astini, 2003; Waisfeld *et al.*, 2023) (Fig. 1). The Puna-Famatina magmatic arc developed to the west is characterized by thick volcanic and sedimentary successions (Coira *et al.*, 1999). In northern Chile, to the south of Salar de Atacama, there are also extensive outcrops of Ordovician volcanic, intrusive, and sedimentary rocks (Niemeyer, 1989).

An extensional phase during the Late Cambrian led to deposition in the Eastern Cordillera of the Mesón Group, which consists of *Skolithos*-rich reddish sandstones and siltstones deposited in tide-dominated environments (*e.g.*, Mángano and Buatois, 1999, 2004). During the latest Cambrian (Furongian, Stage 10) and earliest Ordovician (Tremadocian, Tr1), the establishment of the Puna-Famatinian magmatic arc along the convergent proto-Andean margin, and the subsequent transition from an extensional basin to a retroarc basin, led to deposition of more than 3,500 m-thick marine clastic rocks, now part of the Santa Victoria Group. This succession was affected not only by sea-level fluctuations (*e.g.*, Astini, 2003; Buatois and Mángano, 2003; Buatois *et al.*, 2006) but also by tectonic uplifts due to the arc emplacement (*e.g.*, Bahlburg and Hervé, 1997; Vaucher *et al.*, 2020). Regionally, the Mesón Group is unconformably overlain by the Santa Victoria Group (Turner, 1960), which includes the Santa Rosita (Furongian-Tremadocian) and Acoite (Floian) formations. The Santa Rosita Formation has been formally subdivided into six members named, from base to top: Tilcara, Casa Colorada, Pico de Halcón, Alfarcito, Rupasca, and Humacha (Buatois and Mángano, 2003). The Tilcara and Pico de Halcón members record sedimentation in tidal-dominated settings, filling incised valleys, whereas the Casa Colorada, Alfarcito, and Rupasca members were deposited in wave-dominated open-marine environments, punctuated by storm events.

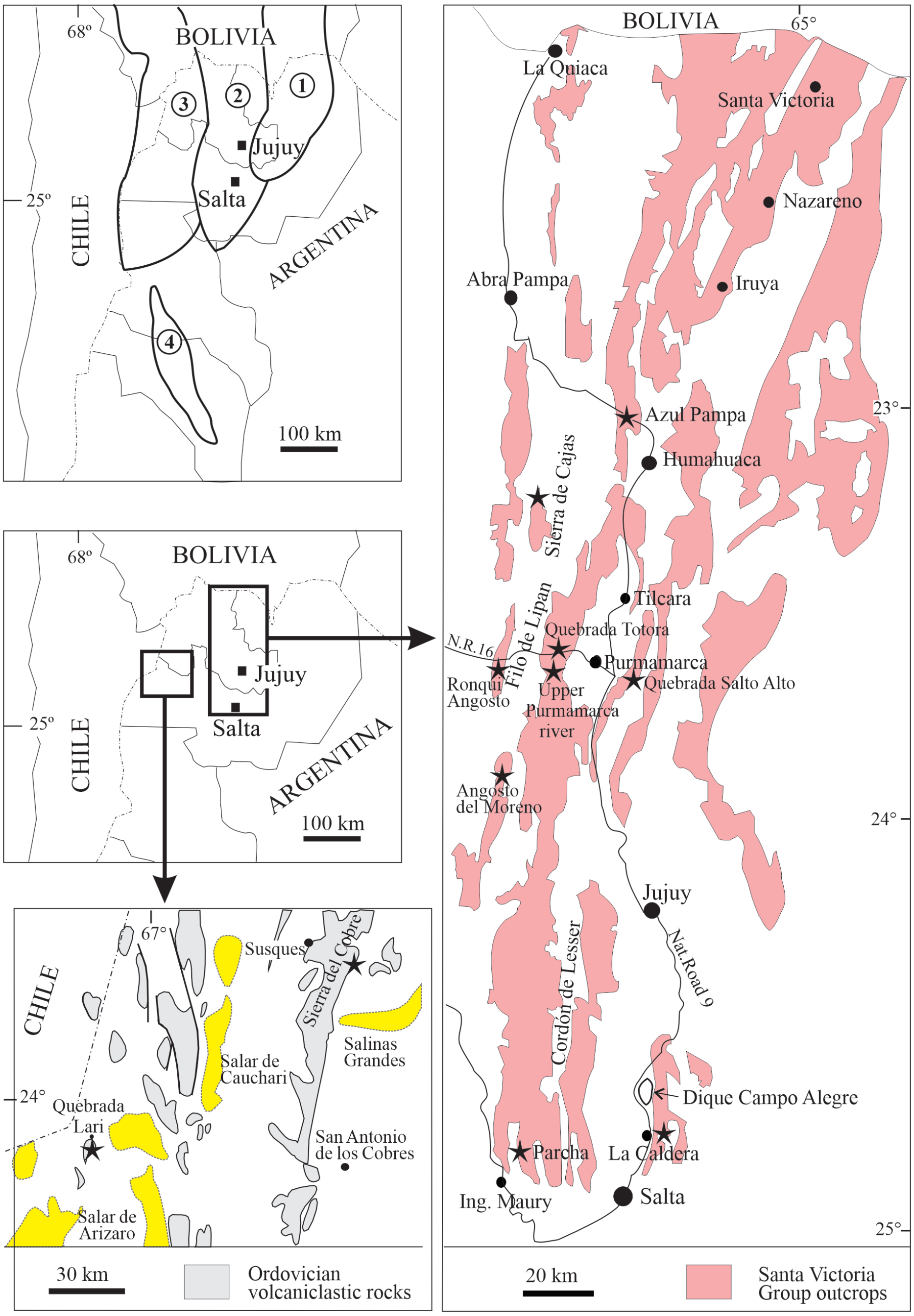


FIG. 1. Map showing the main exposures of the Santa Victoria Group (Furongian-Lower Ordovician) in the Central Andean basin of northwestern Argentina. Upper left map, location of the (1) Subandean Ranges, (2) Eastern Cordillera, and (3) Altiplano-Puna. In the main and bottom left maps, the black stars indicate the localities yielding species of Kvania and Gondwanorthis referred to in the text (see central left map for regional locations). In the bottom left map, yellow areas indicate saline basins. The main roads (black lines) and towns (black circles) are indicated in the main map. The study area (Quebrada Salto Alto) is located at 23°45’ S and 65°28’ W.

The Quebrada Salto Alto, from which the studied specimens of *Kvania lariensis* come from, is located a few kilometers to the east of the Purmamarca town, on the east side of the Río Grande, which runs along the extensive Quebrada de Humahuaca valley (Figs. 1, 2A and B). There, the stratigraphic section starts with the Pico de Halcón Member consisting of several meters of thick-bedded, tabular, and cross-stratified sandstones interpreted as recording subtidal sandbars (Buatois and Mángano, 2003) (Fig. 2C, D). They are overlain in sharp contact by the heterolithic fine-grained deposits of the Alfarcito Member, interpreted as reflecting an extensive transgression flooding an estuarine valley (Buatois *et al.*, 2006). Downstream the Quebrada Salto Alto, the stratigraphic section is faulted and folded so that the preserved thickness of the member reaches about 120 m, approximately half as thick as those in other less deformed sections along the Quebrada de Humahuaca (*e.g.*, Rupasca section). The lower part of the Alfarcito Member is characterized by mudstones and greenish-gray fine-grained rippled sandstones, which represent offshore deposits accumulated in a low-gradient platform affected by fairweather and storm waves (Buatois *et al.*, 2006). A few meters above the base of this member there is a conspicuous ~30 m-thick interval of black shales and fossiliferous, pyrite-rich calcareous mudstones and calcarenites (Fig. 2C, D) partly corresponding to the Purmamarca shales of Harrington and Leanza (1957). These beds yielded well preserved specimens of *Kvania*

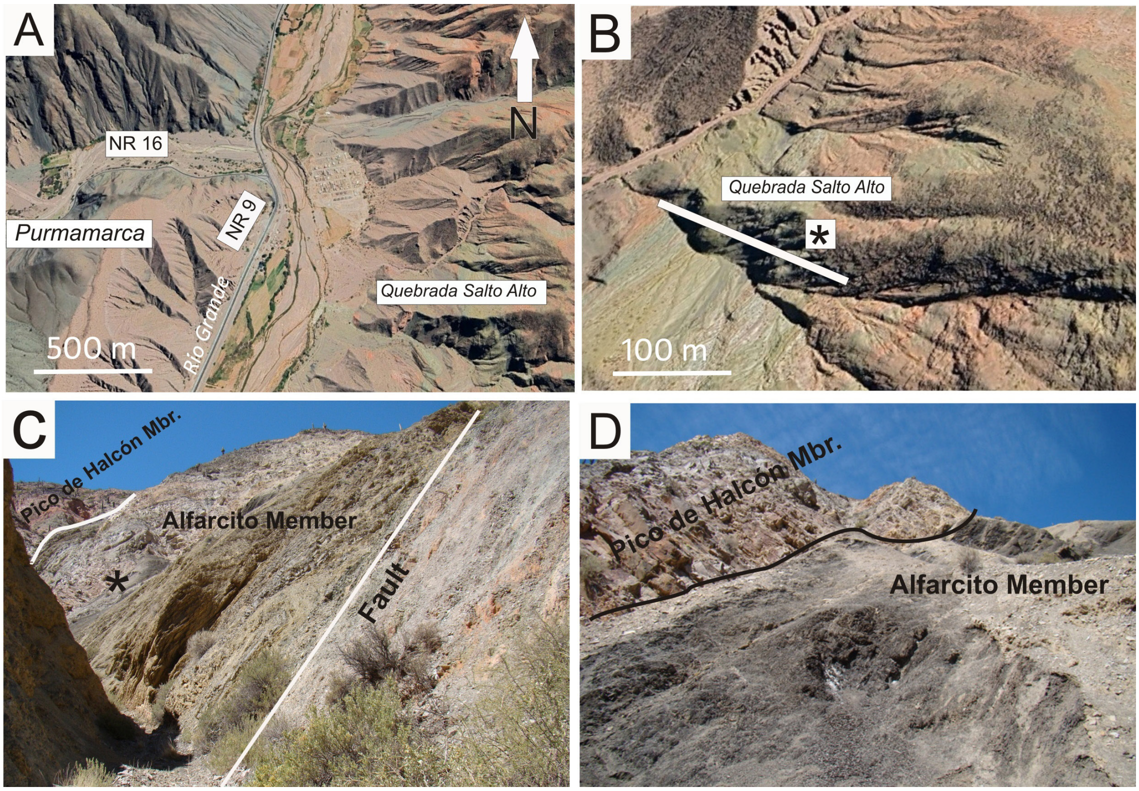


FIG. 2. **A.** Satellite general view of the study area (see Fig. 1 for a general location). **B.** Zoom-in excerpt into the Quebrada Salto Alto showing the stratigraphic section (white line) and fossiliferous beds location (black asterisk). **C.** Headwaters of the Quebrada Salto Alto toward the east, showing the Pico de Halcón and the Alfarcito members. Black asterisk indicates the location of the fossiliferous beds**.** **D.** Detail of the sharp contact between the Pico de Halcón and the Alfarcito members (note that the succession is overturned). In the foreground, fossiliferous black shales with calcareous concretions yielding *Kvania lariensis* and *Jujuyaspis keideli*.

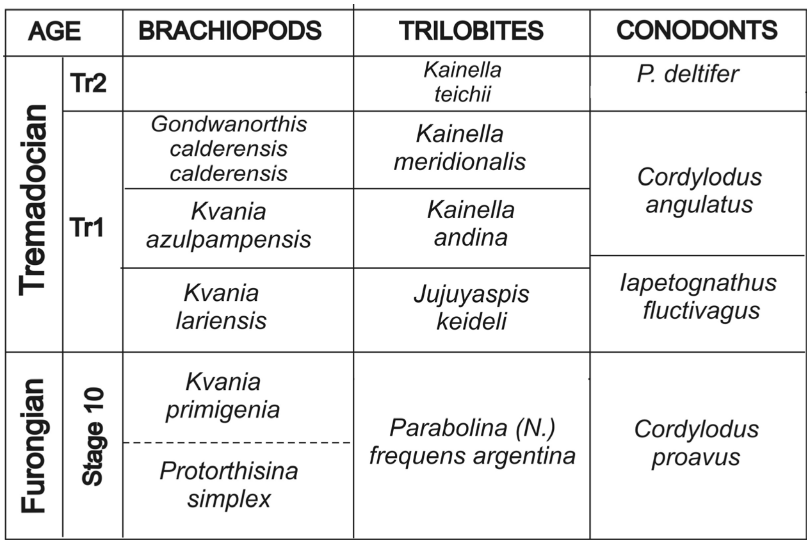
lariensis, *Jujuyaspis keideli* Kobayashi, conodonts (Zeballo and Albanesi, 2009), and linguliformean brachiopods (siphonotretids and obolids). The succession continues with ~80 m of interbedded hummocky cross-stratified fine-grained sandstones and mudstones, the lower ~30 m bearing shell concentrations of *Kvania lariensis*, obolid brachiopods, and trilobites (*Jujuyaspis keideli* and *Asaphellus communis*).

3. The *Protorthisina-Kvania-Gondwanorthis* phylogenetic lineage

The numerous and well-preserved plectorthoid brachiopods recovered from the Upper Cambrian-Floian successions of the Central Andean basin led to recognition of the *Protorthisina-Kvania-Gondwanorthis-Lampazarorthis-Tarfaya* phylogenetic lineage (Benedetto and Muñoz, 2017). Beside cladistic analysis, this evolutionary lineage is supported by ontogenetic evidence, showing that successive taxa display increasingly peramorphic characters affecting shell size, ornament, and internal structures. These findings favored the hypothesis that morphological changes through time were mainly directed by the heterochronic process of peramorphosis (Benedetto, 2007b), consequently constituting a peramorphocline (McNamara, 1990).

The phylogenetic hypothesis supports that the endemic species *Protorthisina simplex* is the ancestral form, which gave rise successively to *Kvania primigenia* Benedetto, *Kvania lariensis* Benedetto, *Kvania azulpampensis* Benedetto, and *Gondwanorthis calderensis* (Benedetto) (Benedetto, 2007b; Benedetto and Muñoz, 2017), thus bracketing the Furongian-lower Tremadocian in the Central Andean basin (Fig. 3). The younger members of the lineage of late Tremadocian-Floian age, *Lampazarorthis bifurcata* (Harrington), *L. alata* Benedetto and Muñoz, *Tarfaya purmamarcaensis* (Benedetto), and *Tarfaya grandis* (Harrington), will be considered in a further analysis, as they are likely to be useful markers for the upper Tremadocian/Floian of the region.

Figure 4 shows the species succession and morphologic changes that took place through the Furongian and early Tremadocian of the Central Andean basin. *Protorthisina simplex* is likely to be the basal taxon of the lineage. It is characterized externally by its minute subcircular shell ornamented by few, up to ten simple ribs, occasionally dichotomized distally. Internally it is distinguished by the brachiophore bases forming a minute septalium. The inferred descendent species Kvania primigenia has a somewhat larger shell and the rib number increases to 18-20. Internally,



AGE		BRACHIOPODS	TRILOBITES	CONODONTS
Tremadocian	Tr2		*Kainella teichii*	*P. deltifer*
	Tr1	*Gondwanorthis calderensis calderensis*	*Kainella meridionalis*	*Cordylodus angulatus*
		Kvania azulpampensis	*Kainella andina*	
		Kvania lariensis	*Jujuyaspis keideli*	*Iapetognathus fluctivagus*
Furongian	Stage 10	*Kvania primigenia*	*Parabolina (N.) frequens argentina*	*Cordylodus proavus*
		Protorthisina simplex		

FIG. 3. Biostratigraphic chart and brachiopod phylozones for the Tremadocian of the Central Andean Basin. Data on conodonts from Rao and Hünicken (1995), Ortega and Albanesi (2005), and Waisfeld *et al.* (2023, and references therein); trilobite biozones from Vaccari *et al.* (2010). Dotted line indicates that the boundary between *Protorthisina simplex* and *Kvania primigenia* is yet to be established (note that *P. simplex* has not been proposed formally as a phylozone).

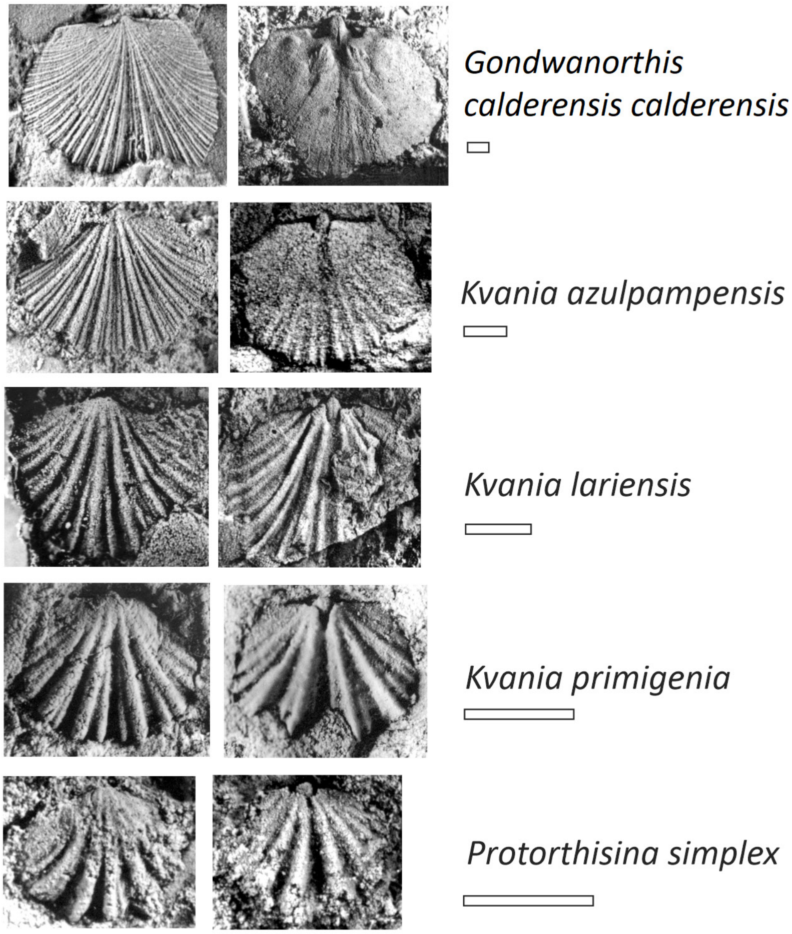


FIG. 4. Phylogenetic lineage of the species discussed in the text showing morphological evolution of the exterior (left) and interior (right) of the dorsal valves (modified from Benedetto, 2007b, and Benedetto and Muñoz, 2017). Scale bars represent 1 mm.

the septalium is larger than in *Protorthisina* and, in later growth stages, brachiophore plates become separated medially (Benedetto, 2007b). This species is morphologically intermediate between *P. simplex* and the succeeding *Kvania lariensis*, in which the rib number increases to 25-30, and the brachiophore bases tend to become subparallel or slightly convergent anteriorly forming a narrow subrectangular notothyrial chamber (Figs. 4 and 5). The latter feature is considered diagnostic of the genus *Kvania*. The next step in the evolutionary lineage is represented by *Kvania azulpampensis*, which always occurs above the last documented appearance of *K. lariensis*. This species is larger than *K. lariensis* and the costellae are more numerous, totalizing up to 45 (Fig. 4). Although the dorsal interiors of both species are quite similar, the notothyrial chamber in *K. azulpampensis* is well developed at all ontogenetic stages. According to the phylogenetic hypothesis detailed here, *K. azulpampensis* gave origin to *Gondwanorthis calderensis* (Benedetto), which is characterized by a variably fascicostellate or parvicostellate ornament forming well-defined bundles distally, the number of costellae counted at valve margin ranging from 65 to 78. The notothyrial chamber in juvenile individuals is small and subrectangular, and it is delimited by blade-like, subparallel brachiophpore plates. As they grow, the lateral apical cavities become gradually filled by secondary deposits masking the brachiophore bases, which are now confined to the posterior part

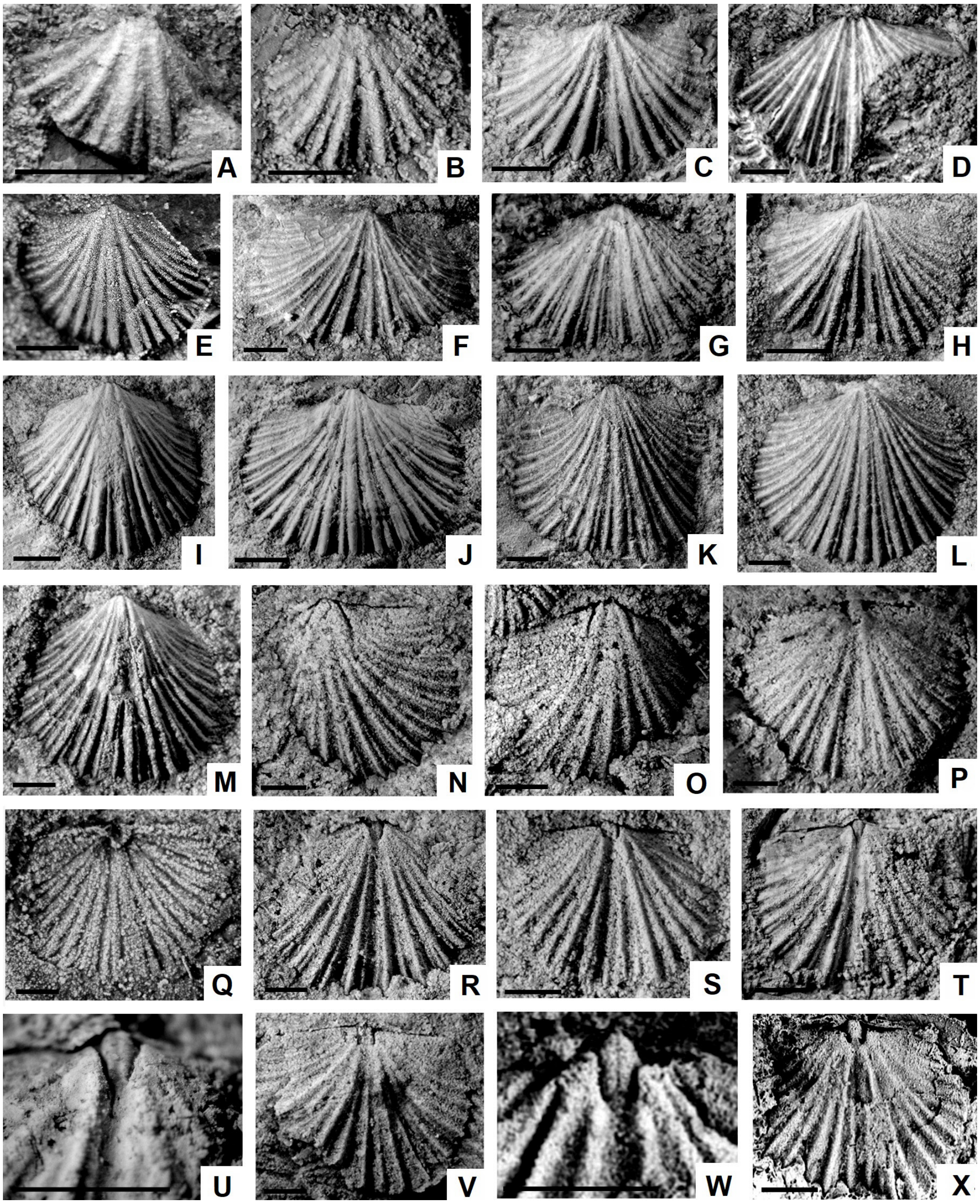


FIG. 5. *Kvania lariensis* from Quebrada Salto Alto, lower part of the Alfarcito Member, Santa Rosita Formation. **A.** Dorsal valve exterior, juvenile specimen CEGH-UNC 27670. **B.** Dorsal valve exterior, young adult specimen, CEGH-UNC 2776. **C.** Dorsal valve exterior, CEGH-UNC 27662. **D.** Dorsal valve exterior, CEGH-UNC 24671. **E.** Ventral valve exterior, latex cast CEGH-UNC 27775. **F.** Dorsal valve exterior, CEGH-UNC 27663. **G.** Dorsal valve exterior, CEGH-UNC 27773. **H.** Dorsal valve exterior, CEGH-UNC 27661a. **I.** Ventral valve exterior CEGH-UNC 27672. **J.** Ventral valve exterior, CEGH-UNC 27660. **K.** Ventral valve exterior CEGH-UNC 27673. **L.** Ventral valve exterior CEGH-UNC 27661b. **M.** Ventral valve exterior CEGH-UNC 27669. **N.** Ventral valve interior, CEGH-UNC 27664b. **O.** Ventral valve internal mold, CEGH-UNC 27665a. **P-Q.** Dorsal valve internal mold and latex cast CEGH-UNC 27667. **R.** Dorsal valve interior CEGH-UNC 27665b. **S.** Dorsal valve interior CEGH-UNC 27674. **T-U.** Dorsal valve interior, and detail of cardinalium, CEGH-UNC 27668. **V.** Dorsal valve interior, CEGH-UNC 27664a. **W-X.** *Kvania lariensis,* specimens from the Las Vicuñas Formation (Quebrada Lari). **W.** Dorsal valve latex cast, detail of cardinalium, CEGH-UNC 18951. **X.** Internal mold of dorsal valve, holotype CEGH-UNC 18948b (from Benedetto, 2007b). Scale bars represent 1 mm. Figured specimens prefixed CEGH-UNC are stored in the paleontological collection of CICTERRA (Centro de Investigaciones en Ciencias de la Tierra, CONICET-UNC), Córdoba, Argentina.

of the notothyrial platform (Fig. 4). It is remarkable that juvenile specimens of *G. calderensis* strongly resemble the adults of *Kvania azulpampensis* in their subrectangular notothyrial chamber flanked by long subparallel brachiophore bases, which suggests that *G. calderensis* originated by peramorphy from *K. azulpampensis* (Benedetto and Muñoz, 2017).

4. Kvania lariensis in time and space

Kvania lariensis Benedetto was described originally from the early Tremadocian Las Vicuñas Formation exposed in the Quebrada Lari, north from the Salar de Arizaro in the western Puna region, a few kilometers from the Chilean border (Fig. 1). In that location, the rocks are intensely folded and faulted and their bases remain unknown. They are unconformably overlain by marine shales and sandstones of latest Ordovician-Early Silurian age (Isaacson *et al.*, 1976; Benedetto and Sánchez, 1990; Rubinstein and Vaccari, 2004).

The Las Vicuñas Formation consists of a lower interval of pyroclastic rocks overlain in sharp contact by a thin bed of fossiliferous calcareous sandstones followed by ~70 m of green shales and mudstones. The type material of *K. larien*sis comes from the lower interval of green shales faulted against the base of the pyroclastic beds, which also contain *Pseudokainella* n. sp. aff. *conica* Kobayashi (formerly referred to as *Kainella* sp. by Moya *et al.*, 1993; see Vaccari and Waisfeld, 2000). The basal calcareous sandstones have yielded conodonts, graptolites, and in particular trilobites of early Tremadocian age, which incluyde *Geragnostus* aff. *intermedius* Palmer, *Asaphellus communis* Robison and Pantoja, *Leiostegium douglasi* Harrington, *Australoharpes* sp., *Onychopyge* sp., *Amzaskiella* sp., and *Conophrys fabiani* Waisfeld *et al.* (Moya *et al.*, 1993; Malanca *et al.*, 1998; Vaccari and Waisfeld, 2000; Waisfeld *et al.*, 2001). These levels also contain the graptolites *Staurograptus* sp. and *Rhabdinopora* sp.

The upper green shales of the Las Vicuñas Formation have been referred tentatively to the *Rhabdinopora flabelliformis parabola* Zone, the second graptolite zone of the Tremadocian Stage (Giuliano *et al.*, 2013). Several calcarenitic levels in there have yielded the conodonts *Cordylodus caboti* Bagnoli, Barnes and Stevens, *Cordylodus intermedius* Furnish, and *Phakelodus tenuis* (Müller) (Rao *et al.,* 2000); more recently, Giuliano *et al.* (2013) documented from the same beds *Cordylodus lindstromi* Druce and Jones, *C. proavus* Müller, *C. deflexus* Bagnoli, Barnes and Stevens, and *Teridontus nakamurai* (Nogami). Such conodont association is indicative of an early Tremadocian age. Therefore, the sum of evidence from the Quebrada Lari stratigraphic section allows placement of *K. lariensis* at the base of the Tremadocian. Data from other localities where this species has been recorded confirm this age placement. For instance, in the Taique Formation at Sierra del Cobre, ~25 km east of Susques (Fig. 1), *K. lariensis* is associated with the trilobite *Jujuyaspis keideli,* a well-established biostratigraphic marker of the base of the Ordovician System in the Central Andean basin (Tortello *et al.*, 2002; Vaccari *et al.*, 2010; Waisfeld *et al.*, 2023, and references therein). In the Ronqui Angosto section, in the westernmost ranges of the Eastern Cordillera (Fig. 1), a few specimens of *K. lariensis* have been found ~80 m above the record of *Protorthisina simplex*, of undoubtedly Furongian age (*Parabolina (Neoparabolina) frequens argentina* Zone). In the Eastern Cordillera of southwestern Bolivia, in turn, a few specimens of *K. lariensis* have been identified in the Iscayachi Formation. A recent revision of the trilobites from this unit at Cuesta de Erquis, ~10 km northwest of Tarija, revealed the presence of an assemblage belonging to the lower part of the *Jujuyaspis keideli* Biozone (lowermost Tremadocian, Tr1), which lies immediately above levels bearing *Parabolina (Neoparabolina) frequens* of Furongian age (Vaccari *et al*., 2018).

The material reported in this paper is the first record of *K. lariensis* in the Quebrada de Humahuaca region (Figs. 1 and 2). In the Quebrada Salto Alto section, like most places, it is associated with *Jujuyaspis keildeli*, which designates a biozone widely distributed in the Central Andean basin marking the base of the Ordovician System (Tortello *et al.*, 2002; Vaccari *et al.*, 2010). Conodonts from the calcareous mudstones yielding *K. lariensis* were referred by Zeballo and Albanesi (2009) to the Late Cambrian *Cordylodus intermedius* Biozone (*Hirsutodontus simplex* Subzone). However, although in certain localities (*e.g.*, Texas and Utah, United States) *H. simplex* is restricted to the Furongian (Miller *et al.*, 2006), in the Green Point GSSP (Newfoundland, Canada) it has been recorded above the first record of *Iapetognathus fluctivagus*, the primary marker of the base of the Ordovician System (Barnes, 1988; Cooper *et al.*, 2001). So, *H. simplex* should be rejected as a marker for the uppermost Cambrian (see discussion in Terfelt *et al.*, 2012).

In accordance with the chronologic evidence mentioned above, *K. lariensis* is proposed here as a marker species for the base of the Ordovician in the Central Andean basin. As figure 3 shows, this phylozone is considered time-equivalent to the *Jujuyaspis keideli* trilobite biozone.

5. The lower Tremadocian brachiopod lineage biozones

Based on the previously exposed phylogenetic evidence, two other phylozones can be recognized within the time slice Tr1 (Bergström *et al.*, 2009), the *Kvania azulpampensis* and the *Gondwanorthis calderensis calderensis* biozones. As figure 3 shows, they are almost equivalent to the *Kainella andina* and *Kainella meridionalis* trilobite biozones (as redefined by Vaccari *et al.*, 2010), respectively, and to the *Cordylodus angulatus* conodont Zone. These two phylozones are described below.

5.1. The *Kvania azulpampensis* Phylozone

The type material of *K. azulpampensis* was recovered approximately 1 km north of the National Road 9 in the Azul Pampa region (Fig. 1), from grey and reddish pink fossiliferous sandstones in the transition between the Casayok and Azul Pampa Formations (Harrington and Leanza, 1957; Fernández, 1985). The succession of mudstones and cross-bedded fine-grained sandstones bearing reworked brachiopod shells, trilobite sclerites, and trace fossils, was referred subsequently to the Alfarcito Member of the Santa Rosita Formation, whereas the overlying parallel-laminated green mudstones (the Azul Pampa Formation) were re-assigned to the Acoite Formation (Such *et al.*, 2007). In the Alfarcito Member, *K. azulpampensis* is associated with the trilobites *Leptoplastides marianus* Harrington and Leanza and *Kainella andina*. *K. azulpampensis* has also been recorded in the upper part of the Pupusa Formation (formerly considered as part of the Cardonal Formation, see Vaucher *et al.*, 2020) exposed at Quebrada Amarilla in the Sierra de Cajas (Fig. 1), where it is associated with *K. andina*. In this section, the first appearance datum (FAD) of *K. andina* lies ~15 m above the last record of *Jujuyaspis keideli* (Vaccari *et al.*, 2010). These beds also mark the FAD of *Anisograptus matanensis*, which occurs a few meters above the first record of *Rhabdinopora flabelliformis* cf. *parabola* (Albanesi and Ortega, 2016).

5.2. The *Gondwanorthis calderensis calderensis* Phylozone

In the Eastern Cordillera, the genus *Gondwanorthis* is one of the most common taxa in strata of late early Tremadocian age. The genus was erected to include some species formerly attributed to the genus *Nanorthis* (Benedetto, 2007b). The type species *Gondwanorthis calderensis* (Benedetto) occurs in many localities of the Eastern Cordillera in strata of early Tremadocian age. In the La Caldera stratotype at the Sierra de Mojotoro, north of Salta City (Fig. 1), this species is associated with trilobites of the *Kainella meridionalis* Zone. In the Parcha locality of the Quebrada del Toro, west of Salta City (Fig. 1), *Gondwanorthis calderensis calderensis* is very abundant in fossil-rich boulders redeposited from the underlying shallow-water cross-bedded sandstones of the Cardonal Formation (see Astini, 2003), which also bear *K. meridionalis* and conodonts of the *Cordylodus angulatus* Biozone (Tortello and Rao, 2000).

The subspecies *G. calderensis alternata* has been recorded in the uppermost part of the Pupusa Formation in the Angosto del Moreno and Sierra de Cajas sections (Fig. 1), associated also with conodonts of the *Cordylodus angulatus* Zone (Rao and Hünicken, 1995; Rao and Tortello, 1998; Rao, 1999; Tortello *et al.*, 1999; Moya *et al.*, 2003). In the Angosto del Moreno stratigraphic section, *G. calderensis alternata* occurs in cross-stratified sandstones and densely packed shell concentrations bearing the rhynchonelliform *Chaniella pascuali* Benedetto and the linguliform brachiopods *Torobolus* cf. *subplanus* Benedetto and Muñoz, *Eurytreta harringtoni* Mergl and Herrera, and *Celdobolus skrikus* Lavié and Benedetto (Benedetto, 2009; Lavié and Benedetto, 2023). These beds also yielded *Kainella morena*, which according to Vaccari *et al.*, 2010 is suggestive of the *Kainella andina* Zone. However, as these authors noted, there is some uncertainty about the exact stratigraphic position of these *Kainella* species because they have not been documented in the same stratigraphic section. In the Sierra de Cajas (Quebrada de la Vizcacha), *G. calderensis alternata* occurs near the top of the Pupusa Formation, a few meters above the last appearance of *Kvania azulpampensis*, supporting a direct ancestor-descendent relationship between the two species.

6. The new Furongian *Kvania primigenia* lineage Biozone

As stated previously, *Protorthisina simplex* is the basal form of the lineage. Its biostratigraphic significance is currently limited by the fact that until the present this species has been found in a single locality and for this reason it has not yet formally proposed as a new biozone. Its Furongian age, however, is beyond doubt and it has been included in the biostratigraphic chart of figure 3. On the contrary, *Kvania primigenia* has been recorded in different localities of the Eastern Codillera, in all cases associated with the trilobite *Parabolina* (*Neoparabolina*) *frequens argentina* (Kayser), which is considered a reliable biostratigraphic marker for the Furongian (Stage 10) of the Central Andean basin (Tortello and Rao, 2000; Tortello *et al.*, 2002; Tortello and Esteban, 2003; Vaccari *et al.*, 2010). The type material of *K. primigenia* comes from dark gray siltstones of the Lampazar Formation at Quebrada Totora (Fig. 1). It also occurs in carbonate lenses within the Lampazar Formation exposed along the old trace of National Road 16 (upper Pumamarca river), in fine-grained sandstones from the lower part of the Santa Rosita Formation (Azul Pampa region) (Such *et al.*, 2007), and in calcareous mudstones exposed at the eastern slope of Sierra de Cajas, in Quebrada Vizcacha, ~130 m above the Padrioc Formation sandstones (Fig. 1). In addition, the Upper Cambrian conodont *Cordylodus proavus* was first reported from these calcareous beds by Rao and Hünicken (1995) and confirmed by subsequent studies (Albanesi and Ortega, 2002; Albanesi *et al.*, 2008, 2015, and references therein). Based on all the available evidence, *K. primigenia* is proposed here as a phylozone, marking the uppermost Cambrian in the Central Andean basin (Fig. 3).

7. Additions to the morphology of *Kvania primigenia* and *K. lariensis*

The numerous specimens of *Kvania lariensis* from the earliest Tremadocian Alfarcito Member in the Quebrada Salto Alto provide new information about its phenotypic variablity (Fig. 5). Morphologically, the new sample of *Kvania lariensis* from the Quebrada Salto Alto does not differ significantly from the type material collected farther west, from the Quebrada Lari area in the western Puna region. The latter, however, is by far much less numerous than the studied sample, so its range of morphological variation cannot be established as accurately. Adult shells from the studied locality are, on average, slightly larger than those from Quebrada Lari, ranging from 3.7 to 6.5 mm in width (in the type specimen"s it ranges from 3.0 to 4.3 mm). Unlike the type material from Quebrada Lari, which includes a single conjoined juvenile specimen (Fig. 7.1 in Benedetto, 2007b), in the studied sample juvenile shells of both valves are relatively frequent. In addition, there are some valves corresponding to young adults and others to large adults, so a reconstruction of the ontogenetic series in possible. Smaller individuals (3.7-3.9 mm in width) are characterized by few (5-6) simple primary costellae dichotomized distally to reach a total of 16-18 at valve margin (Fig. 5A, B). Intermediate ontogenetic stages display 10-11 primary costellae, generating by dichotomy 20-23 costellae at the margin (Fig. 5C). In large adults, primary costae split for a second time at about two-third of valve length, reaching in total ~35 costellae at valve margin. These specimens also show some costellae interpolated between the bundles, especially in the dorsal valve (Fig. 5F, G). In this respect, the material of *K. lariensis* from the Alfarcito Member confirms the trend of increasing number of costellae through ontogeny observed in the type material. This also corrobotates that the lineage as a whole experienced a defined evolutionary trend towards an increase in both shell size and costellae number (Benedetto, 2007b). Internally, the studied material is nearly identical to the type material (compare Fig. 5U and W). Adult specimens from both localities show subparallel brachiophore bases converging onto the valve floor to form a small subrectangular notothyrial chamber (Fig. 5R-T). An incipient septalium, however, can be developed in juvenile individuals (Fig. 5P and Q), as in the adults of the ancestral species *K. primigenia*, supporting its origin by heterochrony.

Concerning the Furongian species *K. primigenia*, a generic assignement is difficult since it exhibits intermediate features between the inferred ancestor *Protorthisina simplex* and its descendent *Kvania lariensis. K primigenia* differs from *P. simplex* mainly in the branching of primary ribs near the mid-valve length and, internally, in its proportionally larger septalium not supported by a septum. Originally, the author questionably referred the type material to *Kvania* because of its fascicostellate ornament rather than simple ribbing, and the fact that in adult specimens the brachiophore bases converge onto the valve floor forming a notothyrial chamber (Benedetto 2007b, p. 277). However, since a true septalium is absent (excepting in some juvenile specimens) and a well-defined subtriangular to subrectangular notothyrial chamber (considered a diagnostic feature of *Kvania*) is always present, the species *primigenia* is herein assigned to *Kvania* without interrogation.

8. Conclusions

Species forming an evolutionary lineage are key to establishing biostratigraphic schemes. In the Central Andean basin of South America, the well-established *Protorthisina-Kvania-Gondwanorthis* brachiopod lineage evolved across the Cambrian-Ordovician boundary. On the basis of well-constrained ages and regional distribution of the successive species, four phylozones are recognized. The species *Kvania primigenia* is proposed as a reliable marker of the uppermost Cambrian, spanning a time almost equivalent to that of the *Parabolina* (*Neoparabolina) frequens argentina* trilobite zone. The species *Kvania lariensis* is reported for the first time from the Eastern Cordillera of Jujuy from beds of well-constrained earliest Tremadocian (Tr1) age. Its presence in the western and eastern Puna regions and in the Eastern Cordillera of Bolivia and northwestern Argentina, along with its well-known conodont-based and graptolite-based age leaves this species as a useful marker for the lowermost Ordovician in the region. The *K. lariensis* and *K. azulpampensis* phylozones are recognized within the time slice Tr1, and are almost time-equivalent to the *Jujuyaspis keideli* and *Kainella andina* trilobite biozones, respectively. Finally, the descendent subspecies *Gondwanorthis calderensis calderensis* is considered coeval to the *Kainella meridionalis* Biozone, marking the upper part of the Tr1 time slice.

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References

Albanesi, G.L.; Ortega, G. 2002. Advances on conodont-graptolite biostratigraphy of the Ordovician System of Argentina. *In* Aspects of the Ordovician System in Argentina (Aceñolaza, F.G.; editor). Instituto Superior de Correlación Geológica (Insugeo), Serie Correlación Geológica 16: 143-165. Tucumán.

Albanesi, G.L.; Ortega, G. 2016. Chapter Two-Conodont and Graptolite Biostratigraphy of the Ordovician System of Argentina. Stratigraphy & Timescales 1: 61-121. https://doi.org/10.1016/bs.sats.2016.10.002

Albanesi, G.L.; Ortega, G.; Zeballo, F.J. 2008. Faunas de conodontes y graptolitos del Paleozoico inferior de la Cordillera Oriental Argentina. *In* Geología y Recursos Naturales de la provincia de Jujuy (Coira, B.; Zapettini, E.O.; editors). Relatorio Congreso Geológico Argentino No. 17: 98-118. Buenos Aires.

Albanesi, G.L.; Giuliano, M.; Pacheco, F.E.; Ortega, G.; Monaldi, C.R. 2015. Conodonts from the Cambrian-Ordovician boundary in the Cordillera Oriental, NW Argentina. Stratigraphy 12: 237-256. http://dx.doi.org/10.29041/strat.12.4.03

Angiolini, L.; Cisterna, G.A.; Mottequin, B.; Shu-Zhong, S.; Muttoni, G. 2021. Global Carboniferous brachiopod biostratigraphy. *In* The Carboniferous Timescale (Lucas, S.G.; Schneider, J.W.; Wang, X.; Nikolaeva, S.; editors). The Geological Society of London, Special Publication 512: 497-550. London. https://doi.org/10.1144/SP512-2020-225

Astini, R.A. 2003. The Ordovician Proto-Andean basins. *In* Ordovician fossils of Argentina (Benedetto, J.L.; editor). Universidad Nacional de Córdoba, Secretaría de Ciencia y Tecnología: 1-74. Córdoba.

Baarli, B.G.; Johnson, M.E. 1988. Biostratigraphy of key brachiopod lineages from the Llandovery Series (Lower Silurian) of the Oslo Region. Norwegian Journal of Geology 68: 259-274.

Bahlburg, H.; Hervé, F. 1997. Geodynamic evolution and tectonostratigraphic terranes of northwestern Argentina and northern Chile. Geological Society of America Bulletin 109 (7): 869-884. https://doi.org/10.1130/0016-7606(1997)109%3C0869:GEATTO%3E2.3.CO;2

Barnes, C. 1988. The proposed Cambrian-Ordovician global Boundary stratotype and point (GSSP) in Western Newfoundland, Canada. Geological Magazine 125 (4): 381-414. http://dx.doi.org/10.1017/S0016756800013042

Benedetto, J.L. 1998a. Early Palaeozoic brachiopods and associated shelly faunas from western Gondwana: their bearing on the geodynamic history of the pre-Andean margin. *In* The proto-Andean margin of Gondwana (Pankhurst, R.J.; Rapela, C.W.; editors). The Geological Society of London, Special Publication 142: 57-83. London. https://doi.org/10.1144/GSL.SP.1998.142.01.04

Benedetto, J.L. 1998b. Early Ordovician (Arenig) brachiopods from the Acoite and Sepulturas formations, Cordillera Oriental, northwestern Argentina. Geologica et Palaeontologica 32: 7-27.

Benedetto, J.L. 2002. The Ordovician brachiopod faunas of Argentina: chronology and biostratigraphic succession. *In* Aspects of the Ordovician System in Argentina (Aceñolaza, F.G.; editor). Instituto Superior de Correlación Geológica (Insugeo), Serie Correlación Geológica 16: 87-106. Tucumán.

Benedetto, J.L. 2005. Hacia un esquema bioestratigráfico de alta resolución para el Cámbrico Superior-Ordovícico del noroeste de Argentina basado en filozonas de braquiópodos rhynchonelliformes. *In* Congreso Geológico Argentino, No. 16, Actas 3: 371-378. La Plata.

Benedetto, J.L. 2007a. Brachiopod succession in the Lower-Middle Ordovician carbonate platform of the Precordillera terrane, western Argentina: an example of interplay between environmental, biogeographic and evolutionary processes. Acta Palaeontologica Sinica 46: 28-36.

Benedetto, J.L. 2007b. New Upper Cambrian-Tremadoc rhynchonelliformean brachiopods from northwestern Argentina: evolutionary trends and early diversification of plectorthoideans in the Andean Gondwana. Journal of Paleontology 81 (2): 261-285. http://dx.doi.org/10.1666/0022-3360(2007)81[261:NUCRBF]2.0.CO;2

Benedetto, J.L. 2009. *Chaniella*, a new lower Tremadocian (Ordovician) brachiopod from northwestern Argentina and its phylogenetic relationships with basal rhynchonelliforms. Paläontologische Zeitschrift 83: 393-405. https://doi.org/10.1007/s12542-009-0023-7

Benedetto, J.L.; Sánchez, M.T. 1990. Fauna y edad del estratotipo de la Formación Salar del Rincón (Eopaleozoico, Puna Argentina). Ameghiniana 27 (3-4): 317-326.

Benedetto, J.L.; Carrasco, P. 2002. Tremadoc (earliest Ordovician) brachiopods from the Purmamarca region and the Sierra de Mojotoro, Cordillera Oriental of northwestern Argentina. Geobios 35 (6): 647-661. https://doi.org/10.1016/S0016-6995(02)00079-7

Benedetto, J.L.; Muñoz, D.F. 2017. Plectorthoid brachiopods from the Lower Ordovician of north-western Argentina; phylogenetic relationships with *Tarfaya* Havlíček and the origin of heterorthids. Journal of Systematic Palaeontology 15 (1): 43-67. https://doi.org/10.1080/14772019.2016.1144086

Benedetto, J.L.; Sánchez, M.T.; Carrera, M.G.; Brussa, E.D.; Salas, M.J. 1999. Paleontológical constraints on successive paleogeographic positions of the Precordillera terrane during the early Paleozoic. *In* Laurentia-Gondwana connections before Pangea (Ramos, V.A.; Keppie, D.; editors). Geological Society of America, Special Paper 336: 21-42. https://doi.org/10.1130/0-8137-2336-1.21

Bergström, S.M.; Chen, X.; Gutiérrez-Marco, J.C.; Dronov, A. 2009. The new chronostratigraphic classification of the Ordovician System and its relations to major regional series and stages and to δ^{13}C chemostratigraphy. Lethaia 42 (1): 97-107. https://doi.org/10.1111/j.1502-3931.2008.00136.x

Buatois, L.A.; Mángano, M.G. 2003. Sedimentary facies and depositional evolution of the Upper Cambrian-Lower Ordovician Santa Rosita Formation in northwest Argentina. Journal of South American Earth Sciences 16 (5): 343-363. https://doi.org/10.1016/S0895-9811(03)00097-X

Buatois, L.A.; Zeballo, F.J.; Albanesi, G.L.; Ortega, G.; Vaccari, E.; Mángano, M.G. 2006. Depositional environments and stratigraphy of the Upper Cambrian-Lower Ordovician Santa Rosita formation at the Alfarcito area, Cordillera Oriental, Argentina: integration of biostratigraphic data within a sequence stratigraphic framework. Latin American Journal of Sedimentology and Basin Analysis 13 (1): 1-29.

Coira, B.; Pérez, B.; Flores, P.; Kay, S.M.; Woll, B.; Hanning, M. 1999. Magmatic sources and tectonic seting of Gondwana margin Ordovician magmas, northern Puna of Argentina and Chile. *In* Laurentia-Gondwana connections before Pangea (Ramos, V.A.; Keppie, J.D.; editors). Geological Society of America, Special Paper 336: 145-170. https://doi.org/10.1130/0-8137-2336-1.145

Cooper, R.A.; Nowlan, E.S.; Williams, S.H. 2001. Global stratotype section and point for the base of the Ordovician System. Episodes 24 (1): 19-28. http://dx.doi.org/10.18814/epiiugs/2001/v24i1/005

Fernández, R.I. 1985. Bioestratigrafía Cambro-Ordovícica del tramo superior de la Quebrada de Humahuaca, provincia de Jujuy, Argentina. *In* Congreso Geológico Chileno, No. 4: 284-308. Antofagasta.

Fortey, R.A. 1988. Seeing is believing: gradualism and punctuated equilibria in the fossil record. Science Progress 72 (1): 1-19.

Giuliano, M.E.; Ortega, G.; Albanesi, G.L.; Monaldi, C.R. 2013. Upper Cambrian/Lower Ordovician conodont and graptolite stratigraphic records in the Lari section, Salar del Rincón, Puna of Salta, Argentina. *In* Conodonts from the Andes (Albanesi, G.L.; Ortega, G.; editors). Asociación Paleontológica Argentina, Publicación Especial 13: 33-37.

Harper, D.A.T.; Villas, E.; Ortega, G. 2004. *Lipanorthis* Benedetto from the Tremadocian of NW Argentina reidentified as dalmanellidine: Significance for the origin and early radiation of punctate orthide brachiopods. Lethaia 37 (3): 271-279. https://doi.org/10.1080/00241160410006537

Harrington, H.J.; Leanza, A.F. 1957. Ordovician trilobites of Argentina. University of Kansas Press, Department of Geology: 276 p. Lawrence.

Havlíček, V. 1994. *Kvania* n. g. and *Petrocrania* Raymond (Brachiopoda, Ordovician) in the Prague basin. Journal of the Czech Geological Society 39 (4): 297-302.

Herrera, Z.A.; Benedetto, J.L. 1991. Early Ordovician brachiopod faunas form the Precordillera basin, western Argentina: biostratigraphy and paleobiogeographical affinities. *In* Brachiopods through time (MacKinnon, D.I.; Lee, D.E.; Campbell, J.D.; editors). A.A. Balkema: 283-301. Rotterdam.

Hunt, G. 2008. Evolutionary patterns within fossil lineages: Model-based assessment of modes, rates, punctuations and process. *In* From Evolution to Geobiology: Research questions driving Paleontology at the start of a new century (Kelley, P.H.; Bambach, R.K.; editors). Paleontological Society Papers 14: 117-131.

Isaacson, P.E.; Antelo, B.; Boucot, A.J. 1976. Implications of a Llandovery (Early Silurian) brachiopod fauna from Salta Province, Argentina. Journal of Paleontology 50 (6): 1103-1112.

Jackson, J.B.C.; Cheetham, A.H. 1999. Tempo and mode of speciation in the sea. Trends in Ecology & Evolution 14 (2): 72-77. https://doi.org/10.1016/s0169-5347(98)01504-3

Jin, J. 2001. Early Silurian stricklandiid brachiopod evolution in eastern North America. *In* Brachiopods: past and present (Brunton; H.; Cocks, L.R.M.; Long, S.L.; editors). Taylor & Francis: 177-188. London.

Laurie, J.R. 1991. Articulate brachiopods from the Ordovician and Lower Silurian of Tasmania. *In* Australian Ordovician brachiopod studies (Jell, P.A.; editor). Memoirs of the Association Australasian Paleontologists 11: 1-106. Brisbane.

Lavié, F.J.; Benedetto, J.L. 2023. Lower Tremadocian (Ordovician) lingulate brachiopods from the Central Andean Basin (NW Argentina) and their biogeographical links. Bulletin of Geosciences 98 (1): 79-93.

Malanca, S.; Monteros, J.A.; Moya, M.C. 1998. Nuevos datos paleontológicos de la Formación Las Vicuñas (Tremadoc temprano), Puna occidental argentina. *In* Congreso Argentino de Paleontología y Bioestratigrafía No. 7: p. 90. Bahía Blanca.

Mángano, M.G.; Buatois, L.A. 1999. Ichnofacies models in Early Paleozoic tide-dominated quartzites: Onshore-Offshore gradients and the classic Seilacherian paradigm. Acta Universitatis Carolinae-Geologica 43 (1): 151-154.

Mángano, M.G.; Buatois, L.A. 2004. Reconstructing Early Phanerozoic intertidal ecosystems: ichnology of the Cambrian Campanario Formation in northwest Argentina. Fossils and Strata 51: 17-38. http://dx.doi.org/10.18261/9781405169851-2004-02

McNamara, K.J. 1990. The role of heterochrony in evolutionary trends. *In* Evolutionary Trends (McNamara, K.J.; editor). Belhaven: 59-74. London.

Miller, J.F.; Ethington, R.L.; Evans, K.R.; Holmer, L.E.; Loch, J.D.; Popov, L.E.; Repetski, J.E.; Ripperdan, R.L.;Taylor, J.F. 2006. Proposed stratotype for the base of the highest Cambrian stage at the first appearance datum of *Cordylodus andresi*, Lawson Cove section, Utah, USA. Palaeoworld 15 (3-4): 384-405. https://doi.org/10.1016/j.palwor.2006.10.017

Mottequin, B.; Brice, D.; Legrand-Blain, M. 2014. Biostratigraphic significance of brachiopods near the Devonian-Carboniferous boundary. Geological Magazine 151 (2): 216-228. https://doi.org/10.1017/S0016756813000368

Moya, M.C.; Malanca, S.; Hongn, F.D.; Bahlburg, H. 1993. El Tremadoc temprano en la Puna occidental Argentina. *In* Congreso Geológico Argentino, No. 12 y Congreso de Exploración de Hidrocarburos, No. 2, Actas 2: 20-30. Mendoza.

Moya, M.C.; Malanca, S.; Monteros, J.A.; Albanesi, G.L.; Ortega, G.; Buatois, L. 2003. Late Cambrian-Tremadocian faunas and events from Angosto del Moreno Section, Eastern Cordillera, Argentina. *In* Ordovician from the Andes (Albanesi, G.L.; Beresi, M.S; Peralta, S.H.; editors). Instituto Superior de Correlación Geológica (Insugeo), Serie de Correlación Geológica 17: 439-444.

Muñoz, D.F.; Benedetto, J.L. 2016. The eoorthid brachiopod *Apheoorthina* in the Lower Ordovician of NW Argentina and the dispersal pathways along western Gondwana. Acta Palaeontologica Polonica 61(3): 633-644. http://dx.doi.org/10.4202/app.00241.2016

Niemeyer, H. 1989. El complejo ígneo-sedimentario del Cordón de Lila, Región de Antofagasta: significado tectónico. Revista Geológica de Chile 16 (2): 163-181.

North American Commission on Stratigraphic Nomenclature. 2005. North American Stratigraphic Code. AAPG Bulletin 89 (11): 1547-1591. https://doi.org/10.1306/07050504129

Ortega, G.; Albanesi, G.L. 2005. Tremadocian graptolite-conodont biostratigraphy of the South American Gondwana margin (Eastern Cordillera, NW Argentina). Geologica Acta 3 (4): 355-371. https://doi.org/10.1344/105.000001383

Rao, R.I. 1999. Los conodontes Cambro-Ordovícicos de la sierra de Cajas y del Espinazo del Diablo, Cordillera Oriental, República Argentina. Revista Española de Micropaleontología 31 (1): 23-51.

Rao, R.I.; Hünicken, M.A. 1995. Conodont biostratigraphy of the Cambrian-Ordovician boundary in northwestern Argentina. *In* Ordovician Odyssey (Cooper, J.D.; Droser, M.L; Finney, S.C; editors), Society of Economic Paleontologist and Mineralogists, Pacific Section 77: 125-128. Fullerton, California.

Rao, R.I.; Tortello, M.F. 1998. Tremadoc conodonts and trilobites from the Cardonal Formation, Incamayo Creek, Salta Province, northwestern Argentina. Palaeontologia Polonica 58: 31-45.

Rao, R.I.; Moya, M.C.; Hünicken, M. 2000. Conodontes en la Formación las Vicuñas (Tremadociano temprano), Puna occidental argentina. Ameghiniana, Suplemento Resúmenes 37 (4): 13-14.

Reyes-Abril, J.; Gutiérrez-Marco, J.C.; Villas, E. 2011. Biostratigraphy of the Middle Ordovician Brachiopods from Central Spain. *In* Ordovician of the World (Gutiérrez-Marco, J.C.; Rábano, I.; García-Bellido, D.; editors). Instituto Geológico y Minero de España: 463-472.

Rubinstein, C.V.; Vaccari, N.E. 2004. Cryptospore assemblages from the Ordovician/Silurian boundary in the Puna region, north-west Argentina. Palaentology 47 (4): 1037-1061. https://doi.org/10.1111/j.0031-0239.2004.00388.x

Sohrabi, A.; Jin, J. 2013. Evolution of the *Rhynchotrema-Hiscobeccus* lineage: implications for the diversification of the Late Ordovician epicontinental brachiopod fauna of Laurentia. Lethaia 46 (2): 188-210. https://doi.org/10.1111/j.1502-3931.2012.00333.x

Sproat, C.D.; McLeod, J.S.A. 2023. Sympatric speciation driving evolution of Late Ordovician brachiopod *Zygospira* in eastern North America. Journal of Paleontology 97 (2): 292-317. https://doi.org/10.1017/jpa.2022.102

Such, P.; Buatois, L.A.; Mángano, M.G. 2007. Stratigraphy, depositional environments and ichnology of the Lower Paleozoic in the Azul Pampa area-Jujuy Province. Revista de la Asociación Geológica Argentina 62 (3): 331-344.

Szduy, K.; Hammann, W.; Villas, E. 2001. The Upper Tremadoc fauna from Vogtendorf and the Bavarian Ordovician from Frankenwald (Germany). Senckenbergiana Lethaea 81: 207-261. https://doi.org/10.1007/BF03043300

Tanaka, S.; Takahashi, A. 2013. The biostratigraphic origin of the theory of punctuated equilibria. Proceedings of the CAPE International Workshops, CAPE Studies in Applied Philosophy & Ethics Series, Vol. 1: 111-126.

Terfelt, F.; Bagnoli, G.; Stouge, S. 2012: Re-evaluation of the conodont *Iapetognathus* and implications for the base of the Ordovician System GSSP. Lethaia 45 (2): 227-237. https://doi.org/10.1111/j.1502-3931.2011.00275.x

Tortello, M.F.; Rao, R.I. 2000. Trilobites y conodontes del Ordovícico temprano del Angosto de Lampazar (provincia de Salta, Argentina). Boletín Geológico y Minero 111 (2-3): 61-84.

Tortello, M.F.; Esteban, S.B. 2003. Trilobites del Cámbrico tardío de la Formación Lampazar (Sierra de Cajas, Jujuy, Argentina). Implicancias bioestratigráficas y paleoambientales. Ameghiniana 40 (3): 323-344.

Tortello, M.F.; Rábano, I.; Rao, R.I.; Aceñolaza, F.G. 1999. Los trilobites de la transición Cámbrico-Ordovícico en la quebrada Amarilla (Sierra de Cajas, Jujuy, Argentina). Boletín Geológico y Minero 110 (5): 3-20.

Tortello, M.F.; Esteban, S.B.; Aceñolaza, G.F. 2002. Trilobites from the base of the Ordovician System in northwestern Argentina. *In* Aspects of the Ordovician System in Argentina (Aceñolaza, G.F.; editor). Instituto Superior de Correlación Geológica (Insugeo), Serie Correlación Geológica 16: 131-142. Tucumán.

Turner, J.C.M. 1960. Estratigrafía de la Sierra de Santa Victoria y adyacencias. Boletín de la Academia Nacional de Ciencias 41 (2): 163-196. Córdoba.

Vaccari, N.E.; Waisfeld, B.G. 2000. Trilobites Tremadocianos de la Formación Las Vicuñas, Puna occidental, Provincia de Salta, Argentina. *In* Memorias Congreso Geológico Boliviano, No. 14: 165-169. La Paz.

Vaccari, N.E.; Waisfeld, B.G.; Marengo, L.; Smith, L. 2010. *Kainella* Walcott, 1925 (Trilobita, Ordovícico Temprano) en el noroeste de Argentina y sur de Bolivia. Importancia Bioestratigráfica. Ameghiniana 47 (3): 293-305.

Vaccari, N.E.; Waisfeld, B.G.; Canelo, H.N.; Smith, L. 2018. Trilobites from the Iscayachi Formation (Upper

Cambrian-Lower Ordovician), Cordillera Oriental, South Bolivia. Biostratigraphic implications. *In* Fósiles y Facies de Bolivia (Suárez Riglos, R.; Dalenz Farjat, A.; Pérez Leyton, M.A.; editors), Yacimientos Petrolíferos Fiscales Bolivianos: 36-58. Santa Cruz de la Sierra.

Vaucher, R.; Vaccari, N.E.; Balseiro, D.; Muñoz, D.F.; Dillinger, A.; Waisfeld, B.G.; Buatois, L.A. 2020. Tectonic controls on late CambrianEarly Ordovician deposition in Cordillera oriental (Northwest Argentina). International Journal of Earth Sciences 109: 1897-1920. https://doi.org/10.1007/s00531-020-01879-9

Villas, E.; Herrera, Z.A. 2004. Revision of the brachiopod *Eoorthis grandis* Harrington, 1938, from the Lower Ordovician of Northwestern Argentina. Ameghiniana 41 (1): 119-123.

Villas, E.; Herrera, Z.A.; Ortega, G. 2009. Early orthid brachiopods from the Tremadocian (Lower Ordovician) of Northwestern Argentina. Journal of Paleontology 83 (4): 604-613. https://doi.org/10.1666/08-165R.1

Waisfeld, B.G.; Vaccari, N.E.; Chatterton, B.D.E.; Edgecombe, G. 2001. Systematic of Shumardiidae (Trilobita), with new species from the Ordovician of Argentina. Journal of Paleontology 75 (4): 827-859. https://doi.org/10.1666/0022-3360(2001)0752.0.CO;2

Waisfeld, B.G.; Benedetto, J.L.; Toro, B.A.; Voldman, G.G.; Rubinstein, C.V.; Heredia, S.; Assine, M.L.; Vaccari, N.E.; Niemeyer, H. 2023. The Ordovician of southern South America. *In* A Global Synthesis of the Ordovician System, Part 2 (Servais, T.; Harper, D.A.T.; Lefebvre, B.; Percival, I.G.; editors). The Geological Society of London, Special Publication 533: 133-173. London. https://doi.org/10.1144/SP533-2022-95

Zeballo, F.J.; Albanesi, G.L. 2009. Conodontes cámbricos y *Jujuyaspis keideli* Kobayashi (Trilobita) en el Miembro Alfarcito de la Formación Santa Rosita, quebrada de Humahuaca, Cordillera Oriental de Jujuy. Ameghiniana 46 (3): 537-556.

Ziegler, A.M. 1966. The Silurian brachiopod Eocoelia hemisphaerica (J. de C. Sowerby) and related species. Palaeontology 9 (4): 523-543.

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