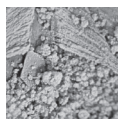


# Lower Tremadocian (Ordovician) lingulate brachiopods from the Central Andean Basin (NW Argentina) and their biogeographical links

FERNANDO J. LAVIÉ & JUAN L. BENEDETTO



A Lower Tremadocian (Tr1) lingulate assemblage from the Guayoc Chico Group (Pupusa Formation) is described and illustrated for the first time. The fauna consists of poorly preserved obolids referred to *Libecoviella?* sp. and *Torobolus* cf. *subplanus* Benedetto & Muñoz, 2015, the acrotretid *Eurytreta harringtoni* Mergl & Herrera, 2015 and the siphonotretid *Celdobolus skrikus* sp. nov. This is the first record of the genus *Celdobolus* in South America, previously recorded from slightly younger strata of Bohemia and Belgium. The Tremadocian lingulate fauna from the Central Andean basin displays closest biogeographical similarity with the Bohemian and Avalonian assemblages and supports a poleward (in Ordovician coordinates) dispersal trajectory along the clastic platforms bordering the Amazonian and NW Africa cratons. On the basis of recent coupled ocean-atmosphere circulation models for the Lower Ordovician it is inferred that larvae could have been transported by the boundary cold-water Antarctica Current. • Key words: Lingulata, Acrotretida, Siphonotretida, Tremadocian, Northwestern Argentina, palaeobiogeography.

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), xxx–xxx (5 figures, 1 table). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received August 5, 2022; accepted in revised form December 5, 2022; published online January 28, 2023; issued XXXXXXXX XX, 2023.

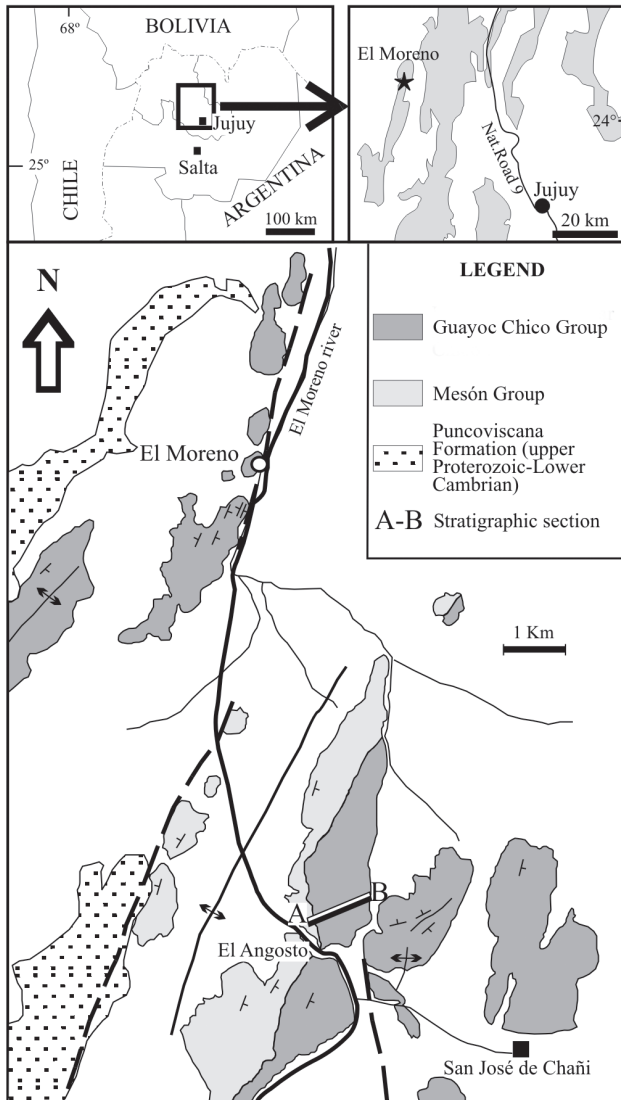
Fernando J. Lavié & Juan L. Benedetto, Centro de Investigaciones en Ciencias de la Tierra (CICTERRA), CONICET and Universidad Nacional de Córdoba, Vélez Sarsfield 1611, X5016GCA Córdoba, Argentina; fernandolavie@gmail.com

The Cambrian–Ordovician linguliform brachiopods from the richly fossiliferous successions of Northwestern Argentina have received increasing attention during recent years, improving our knowledge on these ubiquitous marine organisms. An Upper Cambrian assemblage of lingulids, acrotretids and siphonotretids was described by Mergl *et al.* (2015) from the Lampazar Formation at the Angosto de Lampazar locality. Benedetto & Muñoz (2015) reported several obolid species from the Tremadocian Devendeus and Santa Rosita formations exposed in the Quebrada Humacha and Parcha (Jujuy Province). Later, Benedetto *et al.* (2018) recorded a low diversity brachiopod association dominated by the elkaniid *Broggeria omaguaca* Benedetto & Lavié, 2018 in Benedetto *et al.* (2018), from upper Tremadocian open-shelf mudstones of the Coquena and Santa Rosita formations, in the Santa Victoria and Purmamarca regions. The main goal of this paper is to describe and illustrate a new fauna recovered from the lower Tremadocian Pupusa Formation at Angosto del Moreno, in the Jujuy Province, and to provide a discussion on its biogeographic affinities considering all Tremadocian lingulides identified up to the present from NW Argentina. Such palaeobiogeographic

analysis allows testing the hypothesis of a migratory route linking the Central Andean Basin with north Gondwana and Perunica via the clastic platforms fringing the North African and Brazilian shields (Benedetto & Muñoz 2015).

## Geological setting

In northwestern Argentina, the Cambrian and Ordovician systems are superbly represented by continuous and richly fossiliferous clastic shelf deposits reaching over 3,500 m in thickness. The succession has been referred originally to the Santa Victoria Group (Turner 1960), encompassing the Santa Rosita and the Acoite formations. Stratigraphic nomenclature, however, differs through the basin because of substantial lateral and vertical lithofacial changes (Astini 2003). In the studied area, located on the western slope of the Cordillera Oriental (Fig. 1), the succession has been referred to the Guayoc Chico Group (Ramos 1973), which is coeval with the lower part of the Santa Rosita Formation (Vaucher *et al.* 2020). The Guayoc Chico Group encompasses, from bottom to top, the

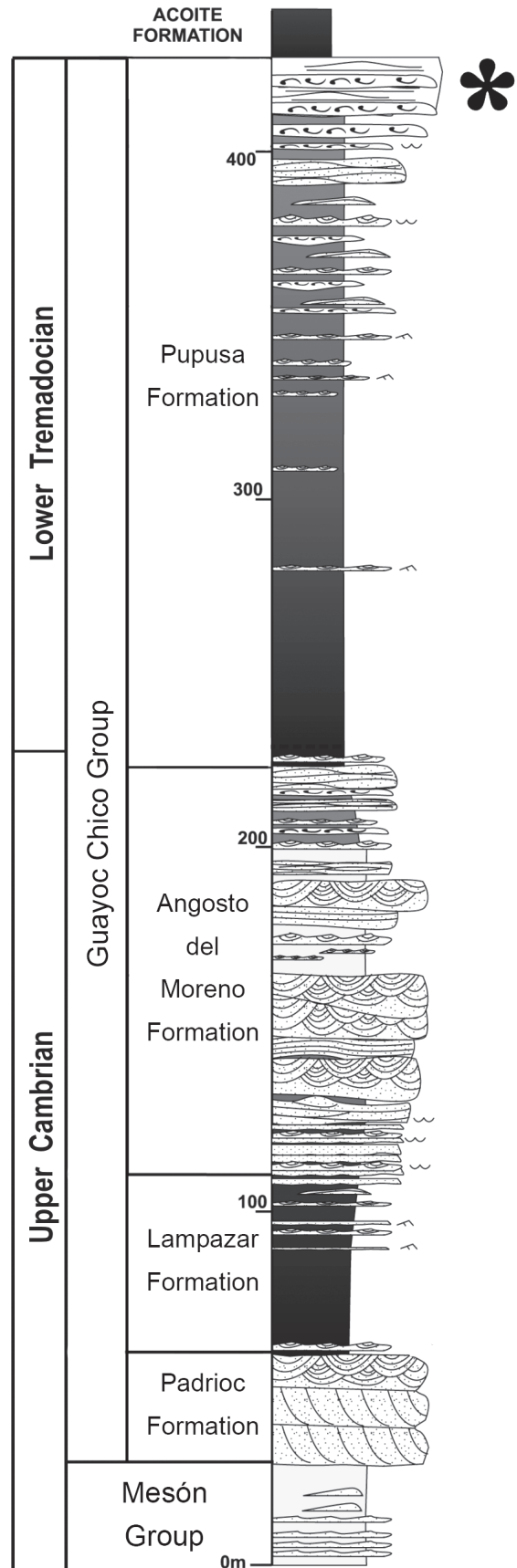


**Figure 1.** General location of the studied area (upper left), distribution of Cambro-Ordovician rocks (grey) in the central Cordillera Oriental (upper right), and geologic sketch of the El Moreno area (modified from Moya *et al.* 2003) showing location of measured stratigraphic section and fossiliferous levels (asterisk).

Padrioc, Lampazar, Angosto del Moreno, and Pupusa formations (Fig. 2), the last two names were proposed by Vaucher *et al.* (2020) to replace the informal stratigraphic units identified preliminarily by Buatois *et al.* (2003).

The fossiliferous beds are exposed at El Angosto locality, about 7 km southeast of El Moreno village (Fig. 1). Here, the Angosto del Moreno Formation consists of

**Figure 2.** Stratigraphic column of Upper Cambrian and Lower Ordovician strata of El Moreno area (modified from Buatois *et al.* 2003 and Astini 2003) showing the horizon bearing the lingulate fauna (asterisk).



shoreface deposits of Furongian age bearing trilobites of the *Neoparabolina frequens argentina* Biozone. The overlying Pupusa Formation, almost 150 m thick, marks the beginning of the Ordovician, encompassing the early Tremadocian *Jujuyaspis keideli* and *Kainella andina* biozones (Vaccari *et al.* 2010). The Pupusa Formation consists of laterally persistent mudstone and siltstone packages interbedded with thin fine-grained sandstones often displaying microhummocky cross-stratified structures. In the fossiliferous locality, the Pupusa Formation culminates with a regressive cycle represented by about 20 m of thin-bedded, fine-grained sandstones passing up into cross-stratified sandstones and densely packed shell concentrations bearing the linguliforms described herein as well as the rhynchonelliforms *Chaniella pascuali* Benedetto, 2009, and *Gondwanorthis calderensis* (Benedetto, 2007) (Benedetto 2009, Benedetto & Muñoz 2017). Shell beds are characterized by a high disarticulation ratio and a low degree of fragmentation. Small and large specimens coexist in the same bed, indicating a relatively poor hydraulic sorting. All these features suggest that specimens have been reworked to some degree but not transported far from their original life habitat. Amalgamated sandstone beds displaying hummocky cross-stratification occasionally pass upwards into trough cross-stratified fine-grained sandstones suggesting deposition in a storm-dominated lower to middle shoreface (Buatois *et al.* 2003, Benedetto 2009, Vaucher *et al.* 2020).

### Biogeographic considerations

Four distinct lower Palaeozoic sedimentary domains can be recognized in southern South America (Benedetto 2018, Waisfeld *et al.* 2023): (1) the intracratonic sedimentary cover of the Amazonian Craton in Brazil, (2) the clastic platforms surrounding the Amazonian Craton and the Pampia terrane, through Peru, Bolivia, and Northwestern Argentina, known as the Central Andean Basin (CAB), (3) the early Palaeozoic subduction-related parautochthonous volcanic arcs and associated volcano-sedimentary basins marginal to Gondwana continent (*e.g.* the Famatina Basin), and (4) the crustal fragments accreted to the proto-Andean margin of Gondwana, of which the better known is the Laurentian-derived Cuyania (or Precordillera) terrane. Each of these regions display significant differences in nature of sedimentary rocks, degree of deformation, preserved stratigraphic record, and biogeographic signature of their fossil faunas. The latter feature has been useful to infer the boundaries between geotectonic units, dispersal pathways around Gondwana, and the probable origin, trajectory and timing of accretion of the Cuyania terrane. Faunal affinities of

the Lower Ordovician rhynchonelliform brachiopods and their palaeogeographic significance have been discussed in several previous papers (*e.g.* Benedetto 1998, 2003; Benedetto *et al.* 2009; Muñoz & Benedetto 2016), whereas biogeographic links of bivalves and trilobites were analyzed to some detail by Waisfeld *et al.* (2003) and Benedetto *et al.* (2009).

With regard to the linguliform brachiopods, the CAB is the sole basin yielding assemblages of Tremadocian age; the remaining of the above mentioned domains only provided Floian or younger faunas. As Popov *et al.* (2013) stated the quality of data of Lower Ordovician linguliforms is variable at global scale, being relatively complete for Laurentia, Baltica, Australia, Avalonia and Kazakhstan, but still incipient for other regions including the South American sector of Gondwana. Another aspect that should be considered in the distribution of linguliforms during the early Ordovician, as pointed out by Bassett *et al.* (1999), is that the group suffers a significant decline in diversity during the later Cambrian and early Tremadocian times after a minor extinction, followed by a recovery during the mid–late Tremadocian. This is mainly seen in micromorphic linguliforms, where there is an increase in diversity and biogeographical differentiation, becoming important components of benthic faunas in marginal environments.

In the present analysis, the known Tremadocian lingulate faunas from the NW Argentina portion of the CAB are compared with other 14 regions of the world bearing approximately coeval assemblages (source of data is shown in the Table 1). Multivariate analysis was performed using the program PAST (Hammer & Harper 2006, Hammer *et al.* 2014). To enhance definition of palaeobiogeographical affinities, both endemic and cosmopolitan genera were excluded from the dataset (Table 1); in addition, those regions with less than three occurrences were excluded from the analysis. In the cluster analysis (Fig. 3A), the Simpson similarity index by unweighted pair group linkage was used to compare associations. In the Principal Coordinates analysis (PCO, Fig. 3B) the eigenvalues are given for the first and second eigenvectors, and these values are plotted in a coordinate system, graphically showing relationships (affinity) between data points (faunal assemblages).

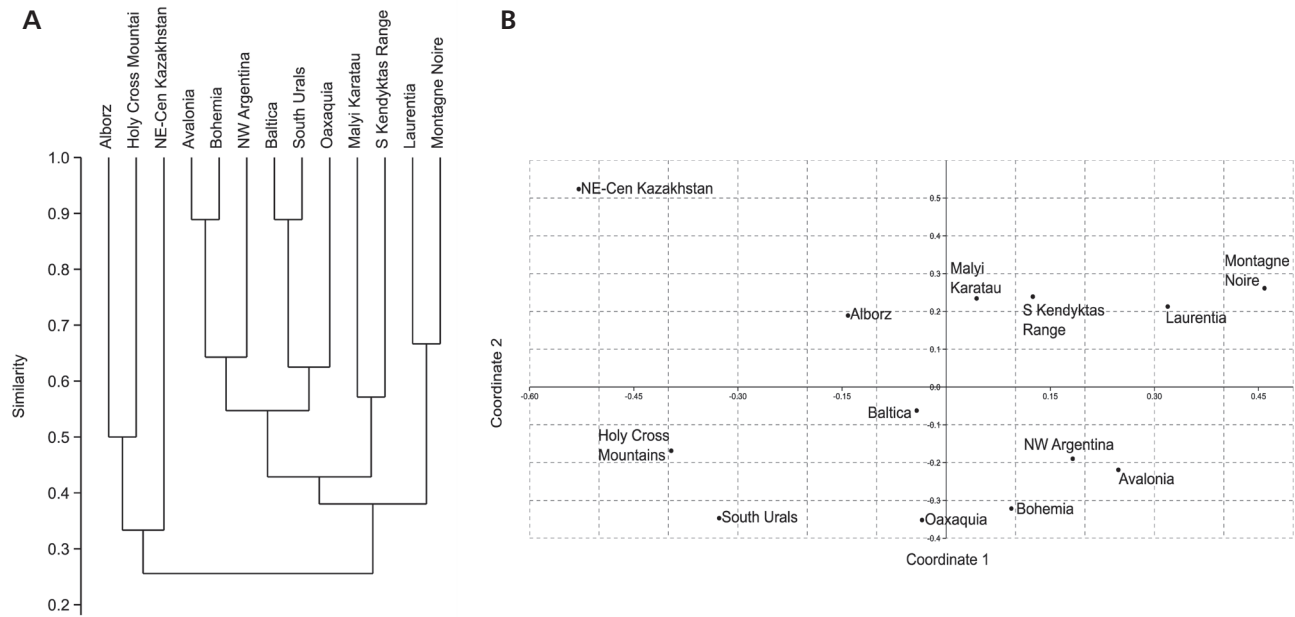
As Figure 3 (A, B) shows, Tremadocian Lingulata from the Central Andean Basin display the closest similarity with the assemblages from Bohemia (Perunica) and Avalonia. Faunas from Baltica, South Urals and Oaxaquia also appear related but with a lower degree of affinity. It is noteworthy that six out of the seven Tremadocian genera occurring in the CAB (~ 86%) are shared with Bohemia. Especially relevant is the presence of the obolids *Leptembolon* and *Libecoviella*, which constitute, together with some other taxa, the *Thysanotos–Leptembolon* Association recorded

**Table 1.** Generic richness of linguliformean brachiopod genera in 15 selected Tremadocian locations. Updated matrix based on the Paleobiology Database (<http://paleobiodb.org>), the Treatise on Invertebrate Paleontology (Holmer & Popov 2000, 2007), Popov *et al.* 2013 and Cocks & Popov 2021. Complementary bibliographic sources: Bohemia (Havlíček 1982, 1989; Mergl 1995, 2002, 2018); Laurentia (Popov *et al.* 2002, Holmer *et al.* 2005, Freeman *et al.* 2018); Avalonia (Sutton *et al.* 1999, 2000; Cocks & Popov 2019); Baltica (Popov & Holmer 1994, 1995; Holmer *et al.* 2000); Alborz (Iran: Popov *et al.* 2008, Ghobadi Pour *et al.* 2011); NW Argentina (Benedetto & Muñoz 2015, Benedetto *et al.* 2018); South Urals (Popov & Holmer 1994, 1995); Australia (Percival & Engelbretsen 2007); Malyi Karatau (Kyrgyzstan: Popov & Holmer 1994, 1995; Holmer *et al.* 2001); S Kendyktas Range (Kazakhstan: Popov & Holmer, 1994); NE–Central Kazakhstan (Northeastern–Central Kazakhstan: Popov & Holmer 1994); Montagne Noire (France: Vizcaino *et al.* 2001); Holy Cross Mountains (Poland: Biernat 1973, Holmer & Biernat 2002); Oaxaquia (Mexico: Streng *et al.* 2011).

	Bohemia	Laurentia	Avalonia	Baltica	Alborz	NW Argentina	Siberia	South Urals	Australia	Malyi Karatau	S Kendyktas Range	NE-Cen Kazakhstan	Montagne Noire	Holy Cross Mts.	Oaxaquia
<i>Acanthambonia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Acrothele</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Acrotreta</i>	1	0	1	1	1	0	0	0	0	0	0	0	1	0	0
<i>Agalattasia</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
<i>Akmolina</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0
<i>Alichovia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Biernatia</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Broeggeria</i>	1	1	1	1	0	1	0	0	0	1	1	0	1	0	0
<i>Celdobolus</i>	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0
<i>Conotreta</i>	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Cristicoma</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
<i>Dactylotreta</i>	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0
<i>Diencobolus</i>	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0
<i>Ditreta</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Divobolus</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Ectenoglossa</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Elliptoglossa</i>	1	0	1	1	1	0	0	0	0	0	1	0	0	0	0
<i>Elkania</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Elkanisca</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Eoconulus</i>	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0
<i>Eopaterula</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Eosiphonotreta</i>	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0
<i>Eurytreta</i>	1	1	1	1	1	1	0	1	0	1	1	0	0	1	1
<i>Expellobolus</i>	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Ferrobolus</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Foveola</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Ghavidelia</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Helmersenian</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Hyperobolus</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Keskentassia</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0

Table 1. Continued.

	Bohemia	Laurentia	Avalonia	Baltica	Alborz	NW Argentina	Siberia	South Urals	Australia	Malvi Karatau	S Kandyktas Range	NE-Cen Kazakhstan	Montagne Noire	Holy Cross Mts.	Oaxaquia
<i>Lamanskya</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Leptembolon</i>	1	0	0	1	0	1	0	1	0	0	0	0	0	1	0
<i>Libecoviella</i>	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Lingulella</i>	0	0	1	1	0	0	0	0	0	0	1	0	0	0	1
<i>Lingulobolus</i>	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Lithobolus</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Longipegma</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Mamatia</i>	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
<i>Mirilingula</i>	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
<i>Oaxaquiatreta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Obolus</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Ombergia</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Orbithele</i>	1	0	1	1	0	0	0	1	0	0	0	0	0	1	0
<i>Otariocunulus</i>	0	0	0	1	0	0	0	1	0	1	0	1	0	0	0
<i>Ottenbyella</i>	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1
<i>Palaeoglossa</i>	1	0	0	1	0	1	0	1	0	0	0	0	0	0	0
<i>Paldiskia</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pidiobolus</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pomeraniotreta</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0
<i>Ralffia</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Rosobolus</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Rowellella</i>	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0
<i>Sasyksoria</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Schizambon</i>	0	1	0	0	0	1	0	0	0	1	1	0	0	0	0
<i>Sedlecilingula</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Semitreta</i>	1	0	1	0	0	0	1	1	0	0	0	0	0	0	1
<i>Siphonobolus</i>	1	0	0	1	0	0	0	1	0	0	0	0	0	1	0
<i>Siphonotretella</i>	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0
<i>Spondyglossella</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Teneobolus</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Thysanotos</i>	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0
<i>Torobolus</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Wahwahlingula</i>	0	1	0	0	1	0	1	0	1	0	0	0	0	0	0
<i>Westonisca</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0



**Figure 3.** A – Simpson similarity index dendrogram. • B – PCO analysis, for the Tremadocian lingulate brachiopods.

in Baltica and in several high-latitude peri-Gondwanan terranes such as Alborz, Perunica, and Central Iran (Mergl 1997a, Bednarczyk 1999, Popov *et al.* 2013). The finding of *Celdobolus* in NW Argentina, which was recorded to date only from Bohemia and Belgium (the latter considered as part of Avalonia, *cf.* Cocks & Fortey, 2009), reinforces the biogeographical links between the CAB and the north Gondwanan continents. The recent discovery in the upper Tremadocian Santa Rosita Formation of NW Argentina of a species close to *Apheoorthina ferrigena* Havlíček, 1949, hitherto only known from the nearly coeval Třenice Formation of the Prague basin, increases the faunal affinities between the two regions (Muñoz & Benedetto 2016). Evidence from the rhynchonelliform faunas from NW Argentina indicates that such a biogeographic pattern persisted into the Floian–Dapingian, during which time Avalonia, North Africa, Bohemia, and CAB form a statistically well-defined cluster (Benedetto *et al.* 2009, fig. 7a). By the Sandbian, rhynchonelliforms from the CAB (NW Argentina and Bolivia) are almost exclusively of Mediterranean type (Benedetto *et al.* 2009, fig. 12).

Evidence from extant linguliformeans led to the inference that Palaeozoic forms had planktotrophic larvae, their longer pelagic larval duration contributing to a potentially broader biogeographic distribution than organisms having lecithotrophic larvae (Sheltema 1986, Freeman & Lundelius 1999). However, larval dispersal is also controlled by environmental factors such as water temperature and depth, and largely by the nature of substrate providing suitable settlement sites (Emig 1997).

Patterns of oceanic circulation are far from linear and vary seasonally, but displacement of larvae takes place essentially along the continents by strong boundary currents, such as the Gulf Stream (Pineda *et al.* 2007). On the basis of inferred Early Ordovician oceanic surface current patterns, Muñoz & Benedetto (2016) suggested a migratory route between the Central Andean Basin and the South European microcontinents along the clastic platforms bordering the Amazonian craton. By the Early Ordovician, the South American Gondwana margin was punctuated by extensive foreland basins filled by clastic sediments derived from both the orogenic belt and the Brazilian Craton (Astini 2003). The large Central Andean Basin of NW Argentina, Bolivia, northern Chile, and southern Peru continues northward (poleward with respect to Ordovician geography) into the subsurface of the Colombian and Venezuelan pre-Andean plains. In turn, these platforms could have been continuous with the clastic deposits of the Taoudeni and Tindouf basins of Morocco (NW Africa), and farther “east” with Avalonia, the Armorican Terrane Assemblage, and Perunica. The continuity between the mid-latitude and high-latitude shelves of “western” Gondwana is clearly shown in the new reconstruction for the Lower Ordovician presented by Cocks & Torsvik (2021, fig. 1). According to the coupled ocean-atmosphere general circulation model produced by Pohl *et al.* (2016) for the Early Ordovician Period (480 Ma) the Central Andean margin was dominated by the cold-water Antarctica Current which could be responsible for larval dispersal from the Andean Gondwana to the high-latitude European microcontinents.

## Material and methods

*Repository and institutional abbreviations.* – Studied specimens are housed in the Centro de Investigaciones en Ciencias de la Tierra (CICTERRA), Consejo Nacional de Investigaciones Científicas y Técnicas, Universidad Nacional de Córdoba, Argentina (acronym CEGH-UNC).

The systematic classification follows that of the Treatise on Invertebrate Paleontology (Holmer & Popov 2000, 2007). The descriptions follow the measurements and terminology introduced by Zhang *et al.* (2018a, b). Photographs were obtained with the Leica MZ7<sub>5</sub> magnifying lens.

## Systematic palaeontology

Class Lingulata Gorjansky & Popov, 1985  
Order Lingulida Waagen, 1885  
Family Obolidae King, 1846

### Genus *Libecoviella* Mergl, 1997a

*Type species.* – *Lingula arachne* Barrande, 1879. Tře-  
nice Formation, Tremadocian. Prague Basin, Czech Re-  
public.

#### *Libecoviella?* sp.

Figure 4A–C

*Material.* – One fragmented ventral valve CEGH-UNC 27398, and two fragmented valves CEGH-UNC 27397, 27399. Additional material: Three fragmented valves not illustrated.

*Remarks.* – Only three incomplete valve fragments were found and referred with doubts to the genus *Libecoviella*. One fragment shows an acuminate posterior region, with well-defined, gently concave ventral pseudointerarea with deep pedicle groove slightly expanding anteriorly, and propleas covered by 9–12 distinct growth lines, lacking flexure lines. Two fragments show the external valve surface, displaying the typical ornamentation of fine closely-spaced terrace lines that form a well-defined zig-zag pattern. The pseudointerarea resembles that seen in *L. tilcarensis* Benedetto & Muñoz, 2015, a common species recorded in the Santa Rosita Formation (lower Tremadocian), from the Quebrada Humacha section (Jujuy Province). Although the Angosto del Moreno specimens closely resemble the species *L. tilcarensis* in the posterior ventral region and pseudointerarea, shell shape and convexity, and exhibit the distinctive ornamentation terrace lines in zig-zag pattern, the generic attribution to *Libecoviella* is not conclusive because of the

lack of information on internal characters and complete valves.

*Occurrence.* – The Angosto del Moreno section (23° 55' 20.00" S, 65° 49' 04.35" W), approximately 10 km southeast of the El Moreno village, Eastern Cordillera, Jujuy Province, Argentina. Lower interval of the Pupusa Formation, Guayoc Chico Group, lower Tremadocian (Tr1, Ordovician).

### Genus *Torobolus* Benedetto & Muñoz, 2015

*Type species.* – *Torobolus subplanus* Benedetto & Muñoz, 2015. Boulders from the Devendeus Formation, lower Tremadocian, Salta Province, Argentina.

#### *Torobolus cf. subplanus* Benedetto & Muñoz, 2015

Figure 4D–E

*Material.* – One dorsal valve CEGH-UNC 27472.

*Description.* – The only specimen available is a dorsal valve showing a gently convex profile, with maximum convexity at posterior third, subcircular outline with rounded posterior margin and length/width ratio 1.1 (up to 11.6 mm long and 10.5 mm wide), with the maximum width located in the anterior third. The anterior and lateral margins are evenly rounded; the posterior margin shows an apical angle averaging 100° and poorly distinguished pseudointerarea. The surface of the valve presents scattered small pits; also shows the arcuate *vascula lateralia* barely recognizable in the posterior third, and traces of the elongated central muscle scars converging to midlength.

*Remarks.* – Although the single dorsal valve from Angosto del Moreno closely resembles *Torobolus subplanus* Benedetto & Muñoz 2015, in shell shape, convexity, and internal features, the attribution to this species is not conclusive because the lack of information on the ventral valve.

*Occurrence.* – The Angosto del Moreno section (23° 55' 20.00" S, 65° 49' 04.35" W), approximately 10 km south-east of the El Moreno village, Eastern Cordillera, Jujuy Province, Argentina. Lower interval of the Pupusa Formation, Guayoc Chico Group, lower Tremadocian (Tr1, Ordovician).

Order Acrotretida Kuhn, 1949  
Family Acrotretidae Schuchert, 1893

### Genus *Eurytreta* Rowell, 1966

*Type species.* – *Acrotreta curvata* Walcott, 1902, Lower Ordovician, Tremadocian, Pogonip Limestone, Eureka district, Nevada, USA.

***Eurytreta harringtoni* Mergl & Herrera, 2015  
in Mergl et al. (2015)**

Figure 4F–Q

2015 *Eurytreta harringtoni* Mergl & Herrera; Mergl, Herrera, Villas & Ortega, 2015, p. 12, figs 9.1–9.20.

**Material.** – Five dorsal valves CEGH-UNC 27455–27459, and two ventral valves CEGH-UNC 27460–27461. Additional material: 81 dorsal valves and 139 ventral valves not illustrated.

**Description.** – Shell ventribiconvex, moderately thick walled and transversely oval in outline, with the valves averaging 83% as long as wide (observed range 66–96%, N = 26). The ventral valve is conical, (median W = 2.66 mm, OR = 1.7–3.8 mm; median L = 2.2 mm, OR = 1.5–2.85 mm; N = 14) and averaging 57% as high as wide (observed range 55–62%, N = 8), with the highest point situated almost on the posterior margin (median H = 1.16 mm, OR = 1–1.3 mm, N = 8), that is straight to slightly convex in dorsal view. The ventral pseudointerarea is apsacline, occupying approximately 30–35% of total width, with a well-defined intertrough. The pedicle foramen is circular, enclosed within the metamorphic shell, is about 0.15 mm in diameter. Ventral interior with an apical process forming a short and low ridge along anterior surface. A pair of raised, elongated oval ventral cardinal muscle scars present on the posterior wall. *Vascula media* prominent, showing a well-developed arcuate mantle canal pattern, consisting of straight, broad and deeply impressed undivided branches, diverging anteriorly and extending slightly beyond the valve midlength. Dorsal valve convex, average width 3.16 mm (OR = 1.35–3.95 mm); average length 2.63 mm (OR = 1.15–3.35 mm, N = 16), showing a barely distinguished broad sulcus. The maximum width is located beyond the valve midlength. The dorsal pseudointerarea is short and occupies less than half of total valve width, average length/width ratio = 0.24 (OR = 0.17–0.28; median W = 1.38 mm; median L = 0.33 mm; N = 9); it has a narrow median groove occupying approximately 25% of pseudointerarea width, limited by anacline to slightly orthocline triangular propareas. Dorsal cardinal muscle scars raised on shell

floor, oval, slightly longer than wide (average length/width ratio 1.48, N = 9), bounded internally by a small thickened ridge; the muscle field is about 56% as long as wide (OR = 46.1–63.6%, N = 9), occupying about 40–68% of total width, and 21–42% of the total length, diverging anteriorly. Small circular anterocentral muscle scars barely distinguished, located in the valve midlength. Low median buttress extends on average 22.5% of total length. Low triangular median septum starting directly anterior to median buttress extends up to 80% of valve length, with maximum height located beyond valve midlength. *Vascula lateralia* with well-defined pinnate pattern, diverging between cardinal and antero-central muscle scars. Metamorphic shell of both valves barely distinguished. Postmetamorphic ornamentation of both valves consists of fine concentric growth lines.

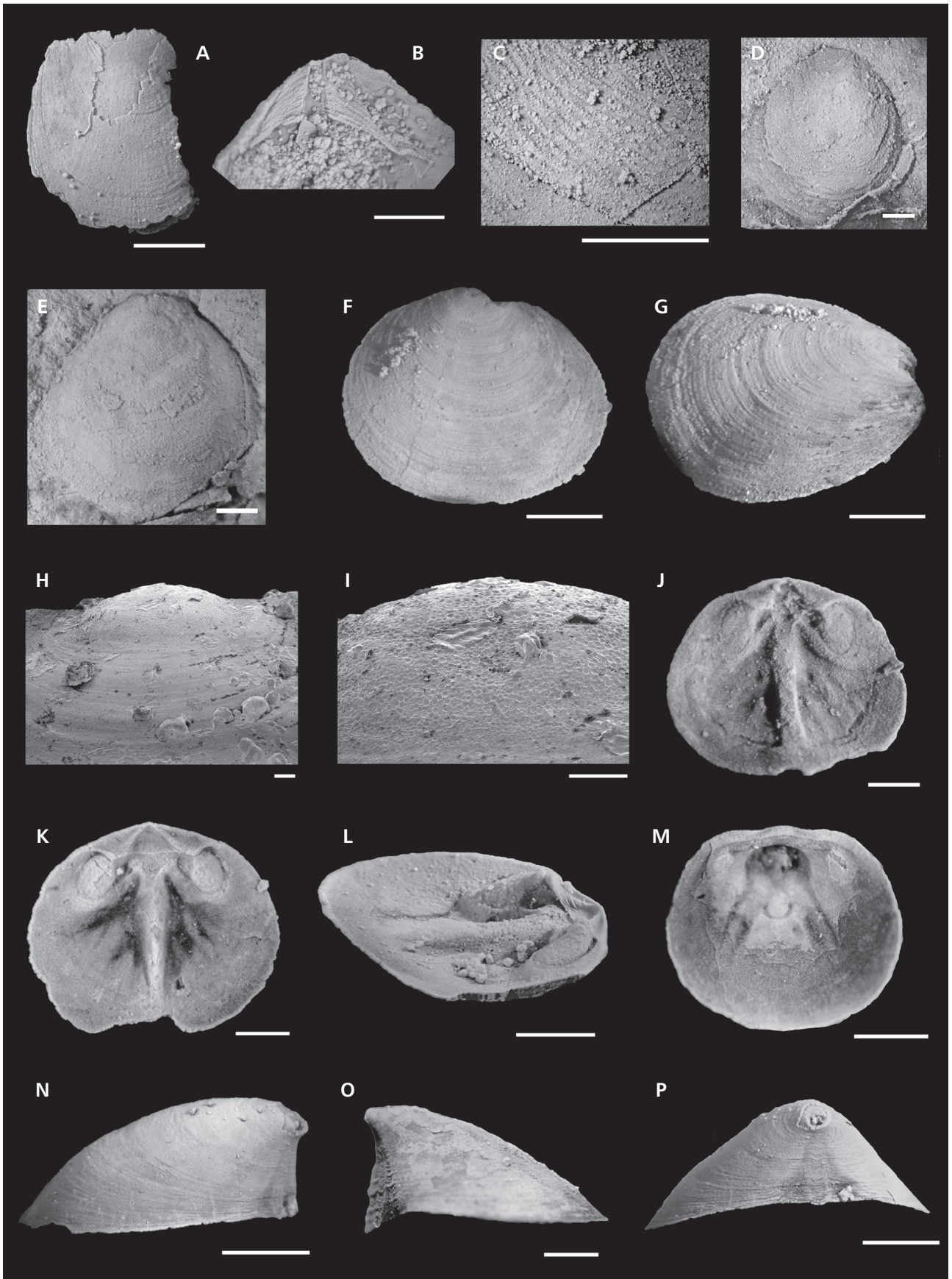
**Remarks.** – The specimens from the Pupusa Formation are closely comparable in most features to *Eurytreta harringtoni* Mergl & Herrera, 2015 in Mergl et al. (2015), from the Lampazar Formation (Furongian, Angosto de Lampazar, Salta Province). They share the convex dorsal valve with broad sulcus and the high conical ventral valve profiles, a transversely oval shell outline, apsacline ventral pseudointerarea and anacline dorsal pseudointerarea, circular pedicle foramen placed within the metamorphic shell, ventral interior with a low apical process along an oval and raised cardinal muscle scars, raised dorsal cardinal muscle field, low median buttress and low triangular median septum, and similar postmetamorphic ornamentation consisting of fine concentric growth lines. *Eurytreta harringtoni* was described originally from the lower part of the Santa Victoria Group at the Parcha locality (Mergl et al. 2015), from beds considered of Furongian age. However, as Muñoz & Benedetto (2016) pointed out, this species is associated with abundant specimens of the plectorthoid *Gondwanorthis calderensis calderensis* (Benedetto 2007), which throughout the basin is confined to the lower Tremadocian *Cordylodus angulatus* conodont Zone (Benedetto 2007, Villas et al. 2009, Benedetto & Muñoz 2017).

**Occurrence.** – Angosto del Moreno section (23° 55' 20.00" S, 65° 49' 04.35" W), approximately 10 km southeast

---

**Figure 4.** A–C – *Libecoviella?* sp.; A – decorticated fragmented valve, CEGH-UNC 27397; B – fragmented ventral valve interior showing the pseudointerarea, CEGH-UNC 27398; C – detail of the postmetamorphic shell ornamentation, CEGH-UNC 27399. • D, E – *Torobolus* cf. *subplanus?* Benedetto & Muñoz, 2015; D – latex cast of the dorsal valve external mold (D) and dorsal valve internal mold (E), CEGH-UNC 27472. • F–P – *Eurytreta harringtoni* Mergl & Herrera, 2015; F–G – dorsal valve in upper view (F) and lateral external view (G), CEGH-UNC 27455; H–I – dorsal valve showing the umbonal region (H) and detail of the micropitted metamorphic ornamentation (I), CEGH-UNC 27456; J – dorsal valve interior, CEGH-UNC 27458; K – dorsal valve interior showing the mantle canal impressions, CEGH-UNC 27457; L – dorsal valve interior in lateral view, CEGH-UNC 27459; M, O – ventral valve interior showing the mantle canals, the apical process and cardinal muscle scars (M), and lateral external view (O), CEGH-UNC 27460; N–P – ventral valve in lateral (N) and posterior views (P), CEGH-UNC 27461. Scale bars = 1 mm; except D, E, which represents 2 mm, and H, I which represents 20 µm.





of the El Moreno village, Eastern Cordillera, Jujuy Province, Argentina. Lower interval of the Pupusa Formation, Guayoc Chico Group, lower Tremadocian (Tr1).

Order Siphonotretida Kuhn, 1949  
Family Siphonotretidae Kutorga, 1848

### Genus *Celdobolus* Havlíček, 1982

*Type species.* – *Obolus complexus* Barrande, 1879. Klabava Formation (Lower Ordovician), Czech Republic.

*Remarks.* – The material described below is assigned to the genus *Celdobolus* based on the combination of several major features, like its equibiconvex lateral profile and subcircular outline, the small pedicle foramen anterior to the apex, a flattened ventral pseudointerarea with orthocline propareas, the absence of inner pedicle tube, an orthocline dorsal pseudointerarea undivided without a median groove, a well-defined muscle scars in both valves, showing particularly a single scar of the anterolateral muscles in the dorsal valve. The material can be distinguished from the genus *Siphonobolus* Havlíček, 1982 due its oval elongated outline and its ventribiconvex profile with a ventral valve more conical than *Celdobolus*. It also possesses a poorly defined pseudointerarea and a long inner pedicle tube, a large dorsal pseudointerarea divided by a wide median groove, and the absence of radial postmetamorphic ornamentation. Some species of *Schizambon* Walcott, 1884 externally resemble the material we refer to as *Celdobolus*, showing radial postmetamorphic ornamentation that forms a reticulated pattern (e.g. *Schizambon obtusus* Holmer, Popov, Streng & Miller, 2005; *Schizambon langei* Freeman, Miller & Dattilo, 2018), although in other species (e.g. *Schizambon cardonalis* Mergl & Herrera, 2015 in Mergl *et al.* 2015) it may not appear on the entire shell surface; however, *Schizambon* presents even dorsibiconvex or ventribiconvex lateral profile, a large pedicle foramen with posterior covered by a plate, a dorsal pseudointerarea divided by a pedicle groove and two separated anterolateral muscle scars in the dorsal inner surface. Another genus that can be compared with our material is *Oxaquatreta* Streng, Mellbin, Landing & Keppie, 2011, which shows similar

postmetamorphic ornamentation reticulated pattern, but differs from *Celdobolus* in having a dorsal sulcus, procline to catacline ventral pseudointerarea divided by a convex ridge, the presence of external pedicle tube and a short dorsal pseudointerarea with median groove. We consider that the sum of internal and external characters identified in the material described below are sufficient to assign it to the genus *Celdobolus*, showing a variant of postmetamorphic shell ornamentation.

### *Celdobolus skrikus* sp. nov.

Figure 5A–M

*Types.* – Holotype: A dorsal valve CEGH-UNC 27462 (Fig. 5A, B, H).

*Type horizon and locality.* – Lower interval of the Pupusa Formation, Guayoc Chico Group, lower Tremadocian (Tr1, Ordovician). The Angosto del Moreno section (23° 55' 20.00" S, 65° 49' 04.35" W), approximately 10 km southeast of the El Moreno village, Eastern Cordillera, Jujuy Province, Argentina.

*Material.* – Paratypes: five dorsal valves CEGH-UNC 27463, 27464, 27466, 27467, 27469, three ventral valves CEGH-UNC 27465, 27468, 27471, and one fragmented material CEGH-UNC 27470. 14 ventral valves and 13 dorsal valves as additional material, not illustrated.

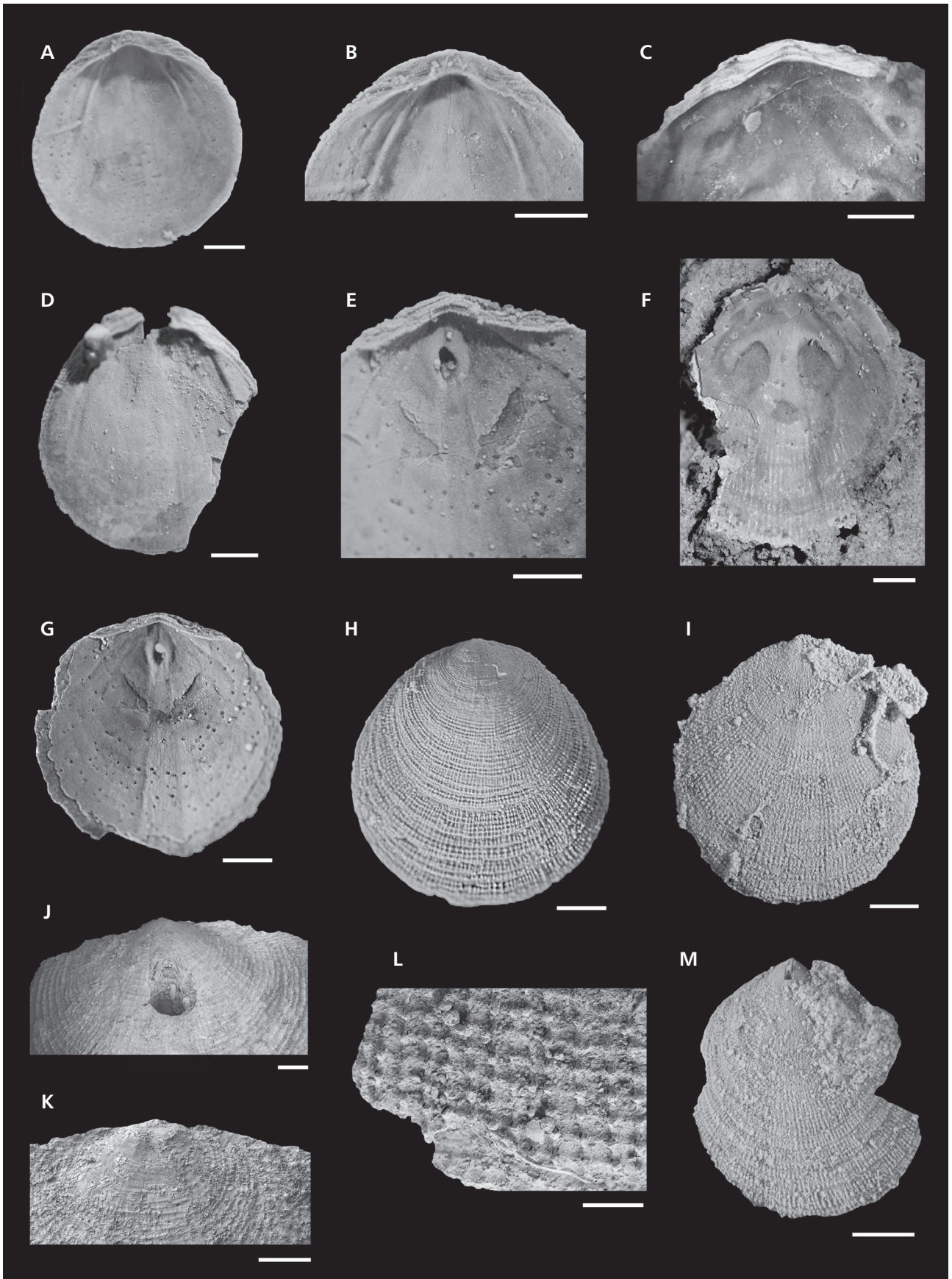
*Etymology.* – From the Norwegian “skrik”, due to the similarity of the painting “The Scream” by Edvard Munch.

*Diagnosis.* – Shell biconvex with subcircular outline and orthocline pseudointerareas. Pedicle foramen present in adult stages, without inner tube. Dorsal inner median ridge absent. Muscle scars in both valves well defined; anterolateral muscles merged into a single scar. Inner surface with anterior and lateral pits. Postmetamorphic radial ornamentation present.

*Description.* – The shell is biconvex in profile, thin to moderately thick walled. Both valves possess subcircular outline, average length/width ratio 1.07 (observed range 1–1.15, N = 14), with the maximum width located at mid-

---

**Figure 5.** A–M – *Celdobolus skrikus* sp. nov.; A, B, H – interior view of the dorsal valve (A), detail of the pseudointerarea and the visceral area (B) and external surface (H), CEGH-UNC 27462 (holotype); C – detail of the middle lateral muscle scars, CEGH-UNC 27463 (paratype); D – fragmented dorsal valve, CEGH-UNC 27464 (paratype), interior surface of dorsal valve showing the muscle scars, CEGH-UNC 27465 (paratype); E, G – detail of the ventral valve posterior region, showing the pedicle foramen and central muscle field (E), and complete inner surface (G), CEGH-UNC 27465 (paratype); F – interior surface of dorsal valve showing the muscle scars, CEGH-UNC 27466 (paratype); I – dorsal valve exterior, CEGH-UNC 27467 (paratype); J – fragmented ventral valve showing the umbonal region, CEGH-UNC 27468 (paratype); K – dorsal valve umbonal region, CEGH-UNC 27469 (paratype); L – fragmented valve showing a detail of the postmetamorphic shell ornamentation, CEGH-UNC 27470 (paratype); M – ventral valve exterior, CEGH-UNC 27471 (paratype). Scale bars = 1 mm; except J, K and L, which represents 200 µm.



length, up to 5.8 mm in the largest specimen. Ventral valve weakly convex, averaging 5.28 mm in length (OR = 3.9–6.1 mm, N = 6) and 4.84 mm in width (OR = 3.5–5.5 mm, N = 6), with the maximum height located in the posterior third. Ventral pseudointerarea smaller than the dorsal, occupying less than two thirds of the total valve width, and approximately 28% as long as wide; it is raised above the valve floor, with orthocline propleas showing a few coarse growth lines. Pedicle foramen elongated oval, with an average length/width ratio of 1.9 and located anterior to apex, with thickened inner edges; inner pedicle tube absent. Central muscle field is 55% as long as wide and located in the posterior third of valve; the muscle scars are large and deeply impressed in the valve surface, oblique and subrectangular in outline (average length/width ratio 2.1) and converging anteriorly to valve midline. Anterior branches of the *vascula lateralia* weakly distinguished. Dorsal valve gently convex and without a sulcus, averaging 5.2 mm in length (OR = 3.25–6 mm, N = 9) and 4.92 mm in width (OR = 3.5–5.5 mm, N = 8) with maximum height in the posterior third. Dorsal pseudointerarea orthocline, widened and forming a platform raised above the valve floor, covered by few growth lines, occupying almost 75% of the total valve width, averaging length/width ratio 0.3 (N = 6); median groove absent making the pseudointerarea undivided; propleas becoming sharper towards the lateral margins, showing weak flexure lines. Posterior half of the visceral area smooth, with the outside lateral and transmedian muscle scars barely distinguishable. Middle lateral muscle scars small and rounded, placed forward of the propleas anterior edges. Central muscle scars oval elongated, located posterolaterally to valve midlength. The anterolateral muscles are attached to form a single circular scar, located almost in the valve center. *Vascula lateralia* weakly defined, arcuate. Internal shell surface with scattered rounded pits located mainly in anterior and lateral areas. Postmetamorphic ornamentation of both valves consists of irregularly spaced concentric growth lines, averaging nine to ten per millimeter, intercalated between coarser growth lamellae, both intersected with radial costellae forming a reticulated pattern. Both valves covered by concentric spines rows; only some of the bases of spines are preserved, located mostly at the intersection between rows and the radial ornamentation.

**Remarks.** – Havlíček (1982) erected the genus *Celdobolus* to group three small siphonotretid species from the Klabava Formation (Floian to Dapingian age) in the Prague Basin (Central Bohemia region). *Celdobolus* cf. *complexus* is mentioned from the upper Tremadocian of the Holy Cross Mountains in Poland (*in* Bednarczyk 1964). Mergl (2002) extensively described and discussed the genus and synonymized the species *C. complexus* and *C. punctatus*. The type species *C. complexus* (Barrande,

1879) differs from *C. skrikus* sp. nov. in having more tear-shaped outline, an anacline ventral pseudointerarea and the pedicle foramen sealed in adult stages, both valves with the inner surface showing coarse granules in marginal areas, and postmetamorphic shell ornamentation lacking radial striation. *Celdobolus mirandus* (Barrande, 1879) can be distinguished from *Celdobolus skrikus* sp. nov. in having a ventral apsacline pseudointerarea, a pedicle foramen located in the terminal position and continued internally as a curved hollow pedicle tube, a dorsal anacline to almost orthocline pseudointerarea, the presence of a median ridge variably developed in the dorsal inner surface and the lack of radial postmetamorphic shell ornamentation. *Celdobolus punctatus* (Klouček, 1924) differs from *C. skrikus* sp. nov. in having an apsacline to catacline ventral pseudointerarea, the presence of coarse tubercles densely crowded on the inner peripheral surface, a broad median ridge or a pair of submedian ridges developed in the ventral visceral area, an anacline dorsal pseudointerarea and a weak median ridge in the dorsal visceral area. Havlíček (1982) referred to *Celdobolus* sp. a single dorsal valve from the Klabava Formation and the lower part of the Šárka Formation (Darriwilian), mentioning that it is more similar to *C. mirandus* than *C. complexus* due to the lack of tubercles on the inner surface. It seems to be more elongated than *C. skrikus* sp. nov. and possesses a median ridge in the visceral area. Recently, Candela & Mottequin (2022) referred to *Celdobolus* sp. new material from the Otré Formation (lower Floian) in Stavelot-Venn Massif of Belgium, but comparison of these specimens is difficult due to the lack of complete shells. It should be noted that the species of *Celdobolus* described herein constitutes the oldest record of the genus, and also is the first record outside Bohemia, Poland and Avalonia.

**Occurrence.** – The same levels and locality as holotype and paratypes.

## Acknowledgements

This paper has benefited considerably from detailed and constructive comments by I. Percival and L.E. Popov as reviewers, and the suggestions made by M. Mergl, as editor. Special thanks to M.J. Salas and I.S. Tapia for their contribution with the photographing of the material and layout of the brachiopod plates. We acknowledge supporting facilities of the Consejo Nacional de Investigaciones Científicas y Técnicas (in particular PUE 2016 CONICET – CICTERRA) and the Universidad Nacional de Córdoba. Financial support was also provided by the CONICET (PIP2020 #11220200102403) and the Agencia Nacional de Promoción de la Investigación, el Desarrollo Tecnológico y la Innovación (PICT-2020-SerieA-02853). This work is a contribution to 653 and 735 IUGS-IGCP projects.

## References

- ASTINI, R.A. 2003. Ordovician basins of Argentina, 1–74. In BENEDETTO, J.L. (ed.) *Ordovician Fossils of Argentina*. Secretaría de Ciencia y Tecnología, Universidad Nacional de Córdoba, Córdoba (Argentina).
- BARRANDE, J. 1879. *Système Silurien du centre de la Bohême. 1<sup>ère</sup> partie. Recherches paléontologiques, vol. 5. Classe des Mollusques. Ordre des Brachiopodes*. 226 pp. Published by the author, Prague & Paris.
- BASSETT, M.G., POPOV, L.E. & HOLMER, L.E. 1999. Organophosphatic brachiopods: patterns of biodiversification and extinction in the early Palaeozoic. *Geobios* 32, 145–63. DOI 10.1016/S0016-6995(99)80026-6
- BEDNARCZYK, W. 1964. The stratigraphy and fauna of the Tremadocian and Arenigian, Oelandian, in the Kielce region of the Holy Cross Mountains, Middle Poland. *Biuletyn Geologiczny* 4, 3–216.
- BEDNARCZYK, W. 1999. Significance of the genus *Thysanotos* Mickwitz, 1986 for the Ordovician stratigraphy of East-Central Europe. *Bulletin of the Polish Academy of Sciences, Earth Sciences* 47, 15–25.
- BENEDETTO, J.L. 1998. Early Palaeozoic brachiopods and associated shelly faunas from western Gondwana: their bearing on the geodynamic history of the pre-Andean margin, 57–83. In PANKHURST, R.J. & RAPELA, C.W. (eds) *The proto-Andean margin of Gondwana*. Geological Society London, Special Publication 142. DOI 10.1144/GSL.SP.1998.142.01.04
- BENEDETTO, J.L. 2003. Early Ordovician (Arenig) brachiopods from volcanoclastic rocks of the Famatina Range, northwest Argentina. *Journal of Paleontology* 77, 212–242. DOI 10.1666/0022-3360(2003)077<0212:EOABFV>2.0.CO;2
- BENEDETTO, J.L. 2007. New Upper Cambrian–Tremadoc rhynchonelliform brachiopods from northwestern Argentina: evolutionary trends and early diversification of Plectrothoidea in Andean Gondwana. *Journal of Paleontology* 81, 261–285. DOI 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. *Palaeontologische Zeitschrift* 83, 393–405. DOI 10.1007/s12542-009-0023-7
- BENEDETTO, J.L. 2018. The strophomenide brachiopod *Ahtiella* Öpik in the Ordovician of Gondwana and the early history of the plectambonitoids. *Journal of Paleontology* 92(5), 768–793. DOI 10.1017/jpa.2018.9
- BENEDETTO, J.L. & MUÑOZ, D.F. 2015. Linguloidean brachiopods from the Lower Ordovician (Tremadocian) of northwestern Argentina. *Bulletin of Geosciences* 90(2), 417–430. DOI 10.3140/bull.geosci.1539
- BENEDETTO, J.L. & MUÑOZ, D.F. 2017. Plectrothoid brachiopods from the Lower Ordovician of north-western Argentina; phylogenetic relationships with *Tarfaya* Havlíček and the origin of heterorthids. *Journal of Systematic Palaeontology* 15, 43–67. DOI 10.1080/14772019.2016.1144086
- BENEDETTO, J.L., VACCARI, N.E., WAISFELD, B.G., SANCHEZ, T.M. & FOGLIA, R.D. 2009. Cambrian and Ordovician paleobiogeography of Andean margin of Gondwana and accreted terranes, 199–230. In BASSETT, M.G. (ed.) *Early Palaeozoic Peri-Gondwanan Terranes: New Insights from Tectonics and Biogeography*. Geological Society London, Special Publication 325. DOI 10.1144/SP325.11
- BENEDETTO, J.L., LAVIÉ, F.J. & MUÑOZ, D.F. 2018. *Broeggeria* Walcott and other Cambrian and Tremadocian linguloid brachiopods from NW Argentina. *Geological Journal* 53, 102–119. DOI 10.1002/gj.2880
- BIERNAT, G. 1973. Ordovician brachiopods from Poland and Estonia. *Palaeontologica Polonica* 28, 1–16.
- BUATOIS, L.A., MOYA, M.C., MÁNGANO, M.G. & MALANCA, S. 2003. Paleoenvironmental and sequence stratigraphic framework of the Cambrian–Ordovician transition in the Angosto del Moreno area, northwest Argentina, 397–401. In ALBANESI, G.L., BERESI, M.S. & PERALTA, S.H. (eds) *Ordovician from the Andes, Proceedings of the 9<sup>th</sup> International Symposium on the Ordovician System, INSUGEO, Serie Correlación Geológica* 17.
- CANDELA, Y. & MOTTEQUIN, B. 2022. Tremadocian and Floian (Ordovician) linguliformean brachiopods from the Stavelot–Venn Massif (Avalonia; Belgium and Germany). *Geologica Belgica* 25, 1–15. DOI 10.20341/gb.2021.007
- COCKS, L.R.M. & FORTEY, R.A. 2009. Avalonia: a long-lived terrane in the Lower Palaeozoic?, 141–155. In BASSETT, M.G. (ed.) *Early Palaeozoic Peri-Gondwanan Terranes: New Insights from Tectonics and Biogeography*. Geological Society London, Special Publication 325. DOI 10.1144/SP325.7
- COCKS, L.R.M. & POPOV, L.E. 2019. Early Ordovician brachiopods from southwest Wales. *Proceedings of the Geologists' Association* 130, 677–90. DOI 10.1016/j.pgeola.2019.02.001
- COCKS, L.R.M. & POPOV, L.E. 2021. The identity and significance of the high-latitude Early Ordovician Mediterranean brachiopod Province. *Geological Magazine* 158, 2187–2208. DOI 10.1017/S001675682100073X
- COCKS, L.R.M. & TORSVIK, T. 2021. Ordovician palaeogeography and climate change. *Gondwana Research* 100, 53–72. DOI 10.1016/j.gr.2020.09.008
- EMIG, C.C. 1997. Ecology of inarticulated brachiopods, 473–495. In WILLIAMS, A., BRUNTON, C.H.C. & CARLSON, S.J. (eds) *Treatise on Invertebrate Paleontology, part H, Brachiopoda, revised, v. 2*. Geological Society of America & University of Kansas Press, Boulder, Colorado & Lawrence, Kansas.
- FREEMAN, G. & LUNDELIUS, J.W. 1999. Changes in the timing of mantle formation and larval life history traits in linguliform and craniiform brachiopods. *Lethaia* 32, 197–217. DOI 10.1111/j.1502-3931.1999.tb00539.x
- FREEMAN, R.L., MILLER, J.F. & DATILO, B.F. 2018. Linguliform brachiopods across a Cambrian–Ordovician (Furongian, Early Ordovician) biomere boundary: the Sunwaptan–Skullrockian North American Stage boundary in the Wilberns and Tanyard formations of central Texas. *Journal of Paleontology* 92, 751–767. DOI 10.1017/jpa.2018.8

- GHOBADI POUR, M., KEBRIAEE-ZADEH, M.R. & POPOV, L.E. 2011. Early Ordovician (Tremadocian) brachiopods from the Eastern Alborz Mountains, Iran. *Estonian Journal of Earth Sciences* 60, 65–82. DOI 10.3176/earth.2011.2.01
- GORJANSKY, V.J. & POPOV, L.E. 1985. Morphology, systematic position and origin of the inarticulate brachiopods with calcareous shells. *Paleontologicheskij Zhurnal* 3, 3–14.
- HAMMER, Ø. & HARPER, D.A.T. 2006. *Paleontological data analysis*. 351 pp. Blackwell Publishing. DOI 10.1002/9780470750711
- HAMMER, Ø., HARPER, D.A.T. & RYAN, P.D. 2014. PAST: Palaeontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica* 4, 9 pp.
- HAVLÍČEK, V. 1949. Orthoidea and Clitambonitoidea of the Bohemian Tremadoc. *Sborník Státního geologického ústavu Československé republiky* 16, 93–144.
- HAVLÍČEK, V. 1982. Lingulacea, Paterinacea, and Siphonotretacea (Brachiopoda) in the Lower Ordovician sequence of Bohemia. *Sborník geologických věd, Paleontologie* 25, 9–82.
- HAVLÍČEK, V. 1989. Climatic changes and development of benthic communities through the Mediterranean Ordovician. *Sborník geologických věd, Geologie* 44, 79–116.
- HOLMER, L.E. & BIERNAT, G. 2002. Lingulate brachiopods from Lower Ordovician (Tremadoc) chalconites, Holy Cross Mountains, Poland. *Acta Palaeontologica Polonica* 47, 141–156.
- HOLMER, L.E., & POPOV, L.E. 2000. Lingulata, 30–146. In WILLIAMS, A., BRUNTON, C.H.C. & CARLSON, S.J. (eds) *Treatise on Invertebrate Paleontology, part H, Brachiopoda, revised*, v. 2. Geological Society of America & University of Kansas Press, Boulder, Colorado & Lawrence, Kansas.
- HOLMER, L.E., & POPOV, L.E. 2007. Linguliformea, 2532–2559. In WILLIAMS, A., BRUNTON, C.H.C. & CARLSON, S.J. (eds) *Treatise on Invertebrate Paleontology, part H, Brachiopoda (revised)*, vol. 7 (supplement). Geological Society of America & University of Kansas Press, Boulder, Colorado & Lawrence, Kansas.
- HOLMER, L.E., POPOV, L.E. & BASSETT, M.G. 2000. Early Ordovician organophosphatic brachiopods with Baltoscandian affinities from the Alay Range, southern Kirgizia. *GFF* 122, 367–375. DOI 10.1080/11035890001224367
- HOLMER, L.E., POPOV, L.E., KONEVA, S.P. & BASSETT, M.G. 2001. Cambrian–early Ordovician brachiopods from Malý Karatau, the western Balkhash Region, and northern Tien Shan, Central Asia. *Special Papers in Palaeontology* 65, 1–180.
- HOLMER, L.E., POPOV, L.E., STRENG, M. & MILLER, J.F. 2005. Lower Ordovician (Tremadocian) lingulate brachiopods from the House and Fillmore formations, Ibex Area, Western Utah, USA. *Journal of Paleontology* 79, 884–906. DOI 10.1666/0022-3360(2005)079[0884:LOTBFB]2.0.CO;2
- KING, W. 1846. Remarks on certain genera belonging to the class Palliobranchiata. *Annals and Magazine of Natural History* 18, 26–42. DOI 10.1080/037454809494387
- KLOUČEK, C. 1924. Nové nálezy z vrstev komárovských. *Sborník Státního geologického ústavu* 4, 199–204.
- KUHN, O. 1949. *Lehrbuch der Paläozoologie*. 326 pp. E. Schweizerbart, Stuttgart.
- KUTORGA, S.S. 1848. Ueber die Brachiopoden-Familie der Siphonotretaceae: *Russische-Kaiserliche Mineralogische Gessellschaft zu St. Petersburg, Verhandlungen 1847 (series 2)*, 250–286.
- MERGL, M. 1995. New lingulate brachiopods from the Milina Formation and the base of the Klabava Formation (late Tremadoc – early Arenig), Central Bohemia. *Věstník Českého geologického ústavu* 70, 101–114.
- MERGL, M. 1997a. Distribution of lingulate brachiopod *Thysanotos* in Central Europe. *Věstník Českého geologického ústavu* 72, 27–35.
- MERGL, M. 1997b. Obolid brachiopods with burrowing sculptures in the Lower Ordovician of Bohemia. *Věstník Českého geologického ústavu* 72, 127–140.
- MERGL, M. 2002. Linguliformean and craniiformean brachiopods of the Ordovician (Třenice to Dobrotivá formations) of the Barrandian, Bohemia. *Acta Musei nationalis Pragae, Series B, Historia Naturalis* 58, 1–82.
- MERGL, M. 2018. Lingulate brachiopods of Tremadocian age from the abandoned Gabriela Mine (Krušná Hora, Central Bohemia, Czech Republic). *Folia Musei rerum naturalium Bohemiae occidentalis. Geologica et Paleobiologica* 52, 7–19. DOI 10.1515/fbgp-2018-0002
- MERGL, M., HERRERA, Z., VILLAS, E. & ORTEGA, G. 2015. Lingulate brachiopods from the Lampazar Formation (late Cambrian) of the Cordillera Oriental of northwestern Argentina. *Journal of Paleontology* 89, 537–552. DOI 10.1017/jpa.2015.42
- MOYA, M.C., MALANCA, S., MONTEROS, J.A., ALBANESI, G.L., ORTEGA, G. & BUATOIS, L.A. 2003. Late Cambrian – Tremadocian faunas and events from the Angosto del Moreno section, Eastern Cordillera, Argentina, 439–444. In ALBANESI, G. (ed.) *Proceedings of the 9<sup>th</sup> International Symposium of the Ordovician System, San Juan*.
- MUÑOZ, D.F. & BENEDETTO, J.L. 2016. The eoarthid brachiopod *Apheoarthina* in the Lower Ordovician of NW Argentina and the dispersal pathways along western Gondwana. *Acta Palaeontologica Polonica* 61(3), 633–644. DOI 10.4202/app.00241.2016
- PERCIVAL, I.G. & ENGELBRETSSEN, M.J. 2007. Early Ordovician lingulate brachiopods from New South Wales. *Proceedings of the Linnean Society of New South Wales* 128, 223–241.
- PINEDA, J., HARE, J.A. & SPONAUGLE, S. 2007. Larval transport and dispersal in the coastal ocean and consequences for population connectivity. *Oceanography* 20, 22–39. DOI 10.5670/oceanog.2007.27
- POHL, A., NARDIN, E., VANDENBROUCKE, T.R.A. & DONNADIEU, Y. 2016. High dependence of Ordovician ocean surface circulation on atmospheric CO<sub>2</sub> levels. *Palaeogeography, Palaeoclimatology, Palaeoecology* 458, 39–51. DOI 10.1016/j.palaeo.2015.09.036
- POPOV, L.E. & HOLMER, L.E. 1994. Cambrian-Ordovician lingulate brachiopods from Scandinavia, Kazakhstan, and South Ural Mountains. *Fossils & Strata* 35, 1–156. DOI 10.1111/j.1502-3931.1994.tb01571.x

- POPOV, L.E. & HOLMER, L.E. 1995. Distribution of brachiopods across the Cambrian–Ordovician boundary on the East European Plate and adjacent areas, 117–120. In COOPER, J.D., DROSER, M.L. & FINNEY, S.C. (eds) *Ordovician Odyssey: Short Papers for the Seventh International Symposium on the Ordovician System*. SEPM, Fullerton, CA, 77.
- POPOV, L.E., HOLMER, L.E. & MILLER, J.F. 2002. Lingulate brachiopods from the Cambrian-Ordovician boundary beds of Utah. *Journal of Paleontology* 76, 211–228. DOI 10.1666/0022-3360(2002)076<0211:LBFTCO>2.0.CO;2
- POPOV, L.E., GHOBADI POUR, M. & HOSSEINI, M. 2008. Early to Middle Ordovician lingulate brachiopods from the Lashkarak Formation, Eastern Alborz Mountains, Iran. *Alcheringa* 32, 1–35. DOI 10.1080/03115510701757126
- POPOV, L.E., HOLMER, L.E., BASSETT, M.G., GHOBADI POUR, M. & PERCIVAL, I.G. 2013. Biogeography of Ordovician linguliform and craniiform brachiopods, 117–126. In HARPER, D.A.T. & SERVAIS, T. (eds) *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society London, Memoir 38. DOI 10.1144/M38.10
- RAMOS, V.A. 1973. Estructura de los primeros contrafuertes de la Puna salto-jujeña y sus manifestaciones volcánicas asociadas, 159–202. In ASOCIACIÓN GEOLÓGICA ARGENTINA (ed.) *Actas del quinto Congreso Geológico Argentino*.
- ROWELL, A.J. 1966. Revision of some Cambrian and Ordovician inarticulate brachiopods. *University of Kansas Paleontological Contributions* 7, 1–36.
- SCHUCHERT, C. 1893. A classification of the Brachiopoda. *The American Geologist* 11, 141–167.
- SHELTEMA, R.S. 1986. On dispersal and planktonic larvae of benthic invertebrates: An eclectic overview and summary of problems. *Bulletin of Marine Science* 39, 290–322.
- STRENG, M., MELLBIN, B.B., LANDING, E. & KEPPIE, J.D. 2011. Linguliform brachiopods from the terminal Cambrian and lowest Ordovician of the Oaxaquia microcontinent (Southern Mexico). *Journal of Paleontology* 85, 122–155. DOI 10.1666/10-074.1
- SUTTON, M.D., BASSETT, M.G. & CHERNS, L. 1999. Lingulate brachiopods from the Lower Ordovician of the Anglo-Welsh basin. Part 1. *Monographs of the Palaeontographical Society London* 154, 1–60. DOI 10.1080/25761900.2022.12131790
- SUTTON, M.D., BASSETT, M.G. & CHERNS, L. 2000. Lingulate brachiopods from the Lower Ordovician of the Anglo-Welsh basin. Part 2. *Monographs of the Palaeontographical Society London* 154, 61–114. DOI 10.1080/25761900.2022.12131793
- TURNER, J. 1960. Faunas graptolíticas de América del Sur. *Revista de la Asociación Geológica Argentina* 14, 1–180.
- VACCARI, N.E., WAISFELD, B.G., MARENGO, L.F. & SMITH, L. 2010. *Kainella* Walcott, 1925 (Trilobita, Ordovícico Temprano) en el noroeste de Argentina y sur de Bolivia. Importancia bioestratigráfica. *Ameghiniana* 47, 293–305. DOI 10.5710/AMGH.v47i3.5
- VAUCHER, R., VACCARI, N.E., BALSEIRO, D., MUÑOZ, D.F., DILLINGER, A., WAISFELD, B.G. & BUATOIS, L.A. 2020. Tectonic controls on late Cambrian/Early Ordovician deposition in Cordillera Oriental (Northwest Argentina). *International Journal of Earth Sciences* 109, 1897–1920. DOI 10.1007/s00531-020-01879-9
- VILLAS, E., HERRERA, Z.A. & ORTEGA, G. 2009. Early orthid brachiopods from the Tremadocian (Lower Ordovician) of Northwestern Argentina. *Journal of Paleontology* 83, 604–613. DOI 10.1666/08-165R.1
- VIZCAÍNO, D., ÁLVARO, J.J. & LEFEBVRE, B. 2001. The Lower Ordovician of the Southern Montagne Noire. *Annales Société Géologique du Nord* 8, 213–220.
- WAAGEN, W. 1885. Salt Range fossils, vol. I, part 4. Productus Limestone fossils, Brachiopoda. *Memoirs of the Geological Survey of India, Palaeontologia Indica* 5, 729–770.
- WAISFELD, B.G., SÁNCHEZ, T.M., BENEDETTO, J.L. & CARRERA, M.G. 2003. Early Ordovician faunal assemblages from western Argentina. Biodiversification trends and palaeogeographic constraints. *Palaeogeography, Palaeoclimatology, Palaeoecology* 196, 343–373. DOI 10.1016/S0031-0182(03)00464-4
- 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 SERVAIS, T., HARPER, D.A.T., LEFEBVRE, B. & PERCIVAL, I.G. (eds) *A Global Synthesis of the Ordovician System, Part 2*. Geological Society London, Special Publication 533. DOI 10.1144/SP533-2022-95
- WALCOTT, C.D. 1884. Paleontology of the Eureka District, Nevada. *U.S. Geol. Survey Monograph* 8, 1–298. DOI 10.5962/bhl.title.23478
- WALCOTT, C.D. 1902. Cambrian Brachiopoda: *Acrotreta*; *Linnarssonella*; *Obolus*; with descriptions of new species. *United States National Museum, Proceedings* 25, 577–612. DOI 10.5479/si.00963801.1299.577
- ZHANG, Z.L., POPOV, L.E., HOLMER, L.E. & ZHANG, Z.F. 2018a. Earliest ontogeny of early Cambrian acrotretoid brachiopods – first evidence for metamorphism and its implications. *BMC Evolutionary Biology* 18, art. 42. DOI 10.1186/s12862-018-1165-6
- ZHANG, Z.L., ZHANG, Z.F., HOLMER, L.E. & CHEN, F.Y., 2018b. Postmetamorphic allometry in the earliest acrotretoid brachiopods from the lower Cambrian (Series 2) of South China and its implications. *Palaeontology* 61, 183–207. DOI 10.1111/pala.12333