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The eoorthid brachiopod *Apheoorthina* in the Lower Ordovician of NW Argentina and the dispersal pathways along western Gondwana

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The eoorthid brachiopod *Apheoorthina* is reported for the first time from the Lower Ordovician of NW Argentina. It is represented by a species similar to *A. ferrigena* from the Tremadocian of the Prague Basin, increasing the faunal affinities between the Central Andean Basin and the South European microcontinents, in particular the Bohemian region (Perunica). Nine out of the fourteen brachiopod genera reported from the Tremadocian of the Central Andean Basin (~64%) are shared with the Mediterranean region, four of which (~28%) have been recorded in the Prague Basin, and two (*Kvania* and *Apheoorthina*) are restricted to the Central Andes and Perunica. Dispersal pathways around Gondwana are analyzed in the light of major factors affecting large-scale distribution of brachiopods (environment, larval capacity for dispersal, oceanic currents). The presence in *Apheoorthina* aff. *ferrigena* of a well-preserved larval protegulum measuring 420 µm in width and 210 µm in length strongly suggests that this species had planktotrophic larvae capable of long-distance dispersal. According to recent ocean-atmosphere general circulation models for the Ordovician Period, the Central Andean margin was dominated by the cold-water Antarctica Current. Despite the complex non-zonal pattern produced by current deflections around the peri-Gondwanan microcontinents, the general westward circulation sense favoured larval dispersal from the Andean region to North Africa, Avalonia, the Armorican Terrane Assemblage, and Perunica. On the other hand, the eastwards flowing Gondwana Current connected the North Gondwana waters with the South American epicontinental seas, which could explain the reversed migration of some brachiopods.

Key words: Brachiopoda, palaeobiogeography, Ordovician, Tremadocian, Gondwana, Perunica, Argentina.

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Introduction

In their biogeographic analysis of the Bolivian brachiopods, Havlíček and Branisa (1980) first noted that the Andean region gradually differentiated from other faunal provinces through the Ordovician as the proportion of Mediterranean (Ibero-Armorican, Bohemian, North African) taxa increased. Since then, numerous species have been published from the Ordovician successions of the large Central Andean Basin encompassing southern Peru, Bolivia, northern Chile, and NW Argentina. Although faunal similarity between the Andean region and the peri-Gondwanan Europe reached a peak during the Sandbian (Benedetto et al. 2009) new evidence demonstrates that faunal exchange between these regions can be traced back to the Tremadocian, and that during the Early Ordovician the Andean region operated as a "species pump" region (sensu Harper et al. 2013) from which new taxa spread to neighbouring areas (Benedetto and Muñoz 2016). The aims of this paper are to report the Bohemian genus *Apheoorthina* in the Tremadocian of NW Argentina, to outline briefly the biogeographic affinities of the Early Ordovician brachiopods from the Central Andes, and to propose an explanation for the faunal similarities of this region with North Gondwana and peripheral south European and Asian terranes taking into account the major factors involved in the present-day brachiopod distribution and the planetary oceanic circulation inferred for Early Ordovician geography.

Institutional abbreviations.—CEGH-UNC, Centro de Investigaciones en Ciencias de la Tierra (CICTERRA), Consejo Nacional de Investigaciones Científicas y Técnicas

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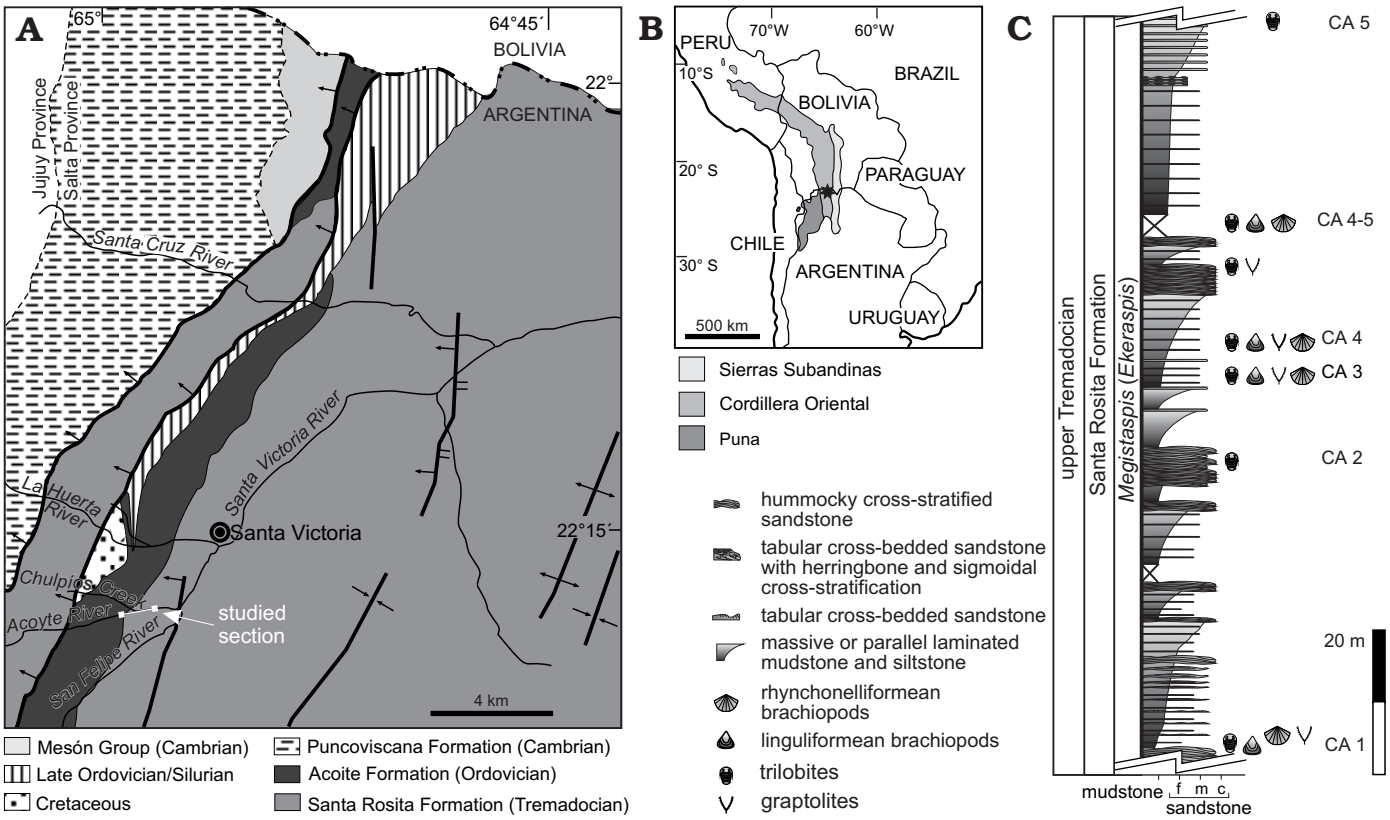

Fig. 1. Location of the studied area (star) within South America (**B**), geological map of the studied area (**A**), and stratigraphic column of the study area (**C**), showing fossiliferous levels.

(CONICET) and Universidad Nacional de Córdoba, Argentina; NML, National Museum Prague, Czech Republic.

Other abbreviations.—pCO_2, carbon dioxide partial pressure; PAL, Present Atmospheric Level.

Geological setting

The widespread, over 3500 m thick upper Cambrian (Furongian)–Lower Ordovician clastic succession of NW Argentina provides an excellent brachiopod record (Benedetto 1998a, 2007b; Benedetto and Carrasco 2002; Villas et al. 2009; Benedetto and Muñoz 2016). The formational subdivision of these deposits, which were included in the Santa Victoria Group by Turner (1960), differs geographically because of marked lateral and vertical lithofacial changes through the basin. In the studied area, the type locality of the Santa Victoria Group, the Furongian–Tremadocian succession has been referred to the Santa Rosita Formation (Turner 1960). This unit unconformably overlies the Cambrian Meson Group which consists of *Skolithos*-rich siltstone and reddish sandstone deposited in tide-dominated environments (Mángano and Buatois 2004).

The studied area is located on the eastern slope of the Cordillera Oriental close to the border with Bolivia, about 3 km southwest the Santa Victoria town. Fossiliferous strata are well exposed along the right margin of the Acoyte River, in front of the mouth of the Chulpíos creek (also known as Chulpiojos or San Luis Creek; Fig. 1). Even though the ca. 100 m sampled interval is limited by faults it can be confidently correlated with the upper part of the Santa Rosita Formation exposed along the La Huerta River near to the Santa Victoria Town (Toro et al. 2015). The stratigraphic succession consists of numerous coarsening and thickening-upward parasequences. The light-grey fine-grained sandstone with hummocky cross stratification bearing abundant shell beds are interpreted as deposited in lower shoreface settings (Fig. 1) whereas the yellowish green mudstone and erosive-based, fine-grained sandstone correspond to offshore-transition deposits. Shell lags and intraclast layers are common at the base of the hummocky beds. The lower offshore deposits consist of greenish grey, massive or parallel-laminated, laterally extensive mudstone beds. Described specimens of *Apheoorthina* aff. *ferrigena* Havlíček, 1949 occur in both the storm-generated shell concentrations and the upper offshore yellowish mudstone.

Apheoorthina aff. *ferrigena* is associated with trilobites of the *Megistaspis* (*Ekeraspis*) Association that has been partially correlated with graptolites of the uppermost part of the *Aorograptus victoriae* Biozone and the lowermost part of the *Araneograptus murrayi* Biozone of upper Tremadocian age (Tr 3 sensu Bergström et al. 2009; see Toro et al. 2015 and references therein).

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Systematic palaeontology

Order Orthida Schuchert and Cooper, 1932

Suborder Orthoidea Woodward, 1852

Superfamily Plectorthoidea Schuchert and LeVene, 1929

Family Eoorthidae Walcott, 1908

Genus *Apheoorthina* Havlíček, 1949

Type species: *Apheoorthina ferrigena* Havlíček, 1949 (by original designation); Třenice Formation, middle Tremadocian; Prague Basin, Czech Republic.

Remarks.—Outside the Czech Republic and NW Argentina, the genus *Apheoorthina* has been reported with interrogation from the lower Floian (*Prioniodus elegans* Zone) of Estonia (Rubel 1961). The Estonian material referred to as *Apheoorthina*? *daunus* (Walcott 1905), however, lacks the typical irregular angular costellae of the genus. Moreover, the notothyrial platform is transversely elongated and non bilobed as in *Apheoorthina* (Rubel 1961: pl. 1: 2).

Apheoorthina aff. *ferrigena* Havlíček, 1949

Figs. 2A–M, 3.

Material.—Seven ventral valves and six dorsal valves, CEGH-UNC 26596–26604, 26915–26918 from the upper Santa Rosita Formation (levels CA1, CA4, CA4-5), upper Tremadocian; road from Santa Victoria to Acoyte, Salta Province, NW Argentina.

Description.—Shell medium sized, up to 17 mm wide, ventribiconvex, transversely semielliptical in outline (average length/width ratio 0.72); maximum width near 1/5 valve length; cardinal extremities obtuse to slightly rounded. Ventral valve moderately convex with a well defined carina on the anterior half. Ventral umbo rounded; beak weakly curved up to the hinge. Dorsal valve slightly convex with a broad sulcus originating at the umbo, corresponding to ventral carina. Dorsal umbo low, inconspicuous. Ornament coarsely fascicostellate consisting of 12−14 subangular, unequal-sized primary costellae originated at the beak, increasing in number mostly by lateral branching on both the medial (slope) and lateral sides of parental costae, sporadically by dichotomy; size and height of costellae diminishes towards the posterolateral areas. Interespaces subangular, of similar width to primary costellae bearing 2−5 finer unbranched ribs. Entire shell surface covered by fine radial striae with 8−10 in 100 μm; concentric ornamentation consists of evenly spaced filae and growth lamellae sporadically developed near the valve margins.

Ventral interior with thin dental plates supporting small, bluntly triangular teeth extending anteriorly into low convergent ridges bounding almost completely a subpentagonal muscle field extended for 20−25% valve length. Muscle field divided longitudinally by a thin septum; adductor and diductor scars undifferentiated. Interior of dorsal valve with subrectangular, concave, anteriorly bilobed notothyrial platform, slightly elevated anteriorly above valve floor extending anteriorly for 15−20% valve length. Cardinal process a simple rounded ridge slightly enlarged anteriorly. Muscle field and vascular system not impressed.

Remarks.—The Santa Victoria specimens are very similar to the type material of *Apheoorthina ferrigena* of Havlíček (1949) and additional material illustrated by Havlíček (1977) from the Třenice Formation of the Prague Basin. In size, outline and ornamentation the Argentinean material is indistinguishable from the Bohemian species. Internally both species are also very similar, excepting that in the Andean specimens the notothyrial platform is less elevated on the valve floor and the ventral muscle bounding ridges are less prominent. In addition, in our material the muscles scars are not impressed and internal ribbing is marked on the entire valve. We consider that such differences may be attributed to preservation since the Bohemian material is preserved in haematitic sandstone and the Andean material comes from mudstone and calcareous siltstone. Our specimens also resemble *Apheoorthina bohemica* Havlíček, 1949, which is from the same haematite lenses at the base of the Třenice Formation yielding *A. ferrigena*. The dorsal interiors of the two Bohemian species are nearly identical; the ventral interiors of *A. bohemica* are not known and thus cannot be compared. According to Havlíček (1977) *A. bohemica* can be distinguished from *A. ferrigena* in having more numerous ribs in the interspaces. However, the ornamentation pattern of both species shows a broad overlap (compare ventral exteriors of *A. bohemica* and *A. ferrigena* illustrated by Havlíček 1977: pl. 4: 3 and pl. 4: 8, respectively), so this feature is taxonomically indecisive. It is noteworthy that the Argentinean material displays a similar range of variation, some specimens having ornamentation of *A. bohemica* type and others of *A. ferrigena* type (cf. Fig. $2B_2$ and I). Because the strong variation in the ornamentation and in absence of substantial internal differences *A. ferrigena* and *A. bohemica* should be considered as conspecific.

Discussion

Inference about *Apheoorthina* larval feeding.—Freeman and Lundelius (1999, 2005, 2008a, b) demonstrated that larval feeding (lecithotrophic or planktotrophic) of Palaeozoic brachiopods can be deduced from the size of the first-formed shell or protegulum. On the basis of the study of larval development in extant brachiopods and the correlation between egg diameter and protegular size they showed that fossil members of the three major brachiopod groups (Linguliformea, Craniiformea, and Rhynchonelliformea) had planktotrophic larvae. In certain specimens the protegulum shows a small embryonic region surrounded by a larger larval region that is delimited from the brephic shell by a lamellar ring. Freeman and Lundelius (2005) concluded that a protegular width less than 175 μm indicates a lecithotrophic larva, whereas species

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Table 1. Record of the Early Ordovician Central Andean Basin brachiopods in North Gondwana, European microcontinents (plus Iran), Baltica, and Australasia. 1, early Tremadocian; 2, late Tremadocian; 3, Floian; ×, present in the indicated time interval; +, present in strata younger than Floian.

	Central Andean Basin			North Africa			Armorica Terrane Assemblage			Avalonia			Perunica			Iran			Baltica			Australasia		
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Chaniella	×																							
Gondwanorthis	×															×								
Kvania	×													×										
Lampazarorthis	×																							
Torobolus	×																							
Apheoorthina		×												×										
Astraborthis		×										×												
Ectenoglossa		×						×			×													
Leptembolon		×												×						×				
Lesserorthis		×																						
Libecoviella	×	×												×									×	
Lipanorthis		×	×						+															
Nothorthisina		×																						
Tarfaya		×	×			×											×						×	×
Ahtiella			×									×									+			
Camerella			×																					
Desmorthis			×									+												
Euorthisina			×			×						×			+									
Glyptorthis			×									+												
Hesperonomia			×						×			×												
Incorthis			×			×																		
Paralenorthis			×						×			×					×				+			

with protegula width more than 225 µm are regarded as having had planktotrophic larvae.

In one dorsal valve of *Apheoorthina* aff. *ferrigena* recovered from a calcareous shell concentration (level CA4-5; Fig. 1) the protegulum is well preserved. The larval protegulum is delimited from the brephic shell by a conspicuous lamella (Fig. 3). The lack of growth lines confirms its identification as a protegulum (Popov et al. 2007). An apical region ca. 180 µm in diameter raised above the larval protegulum and delimited by a shell discontinuity is interpreted as the embryonic protegulum (Fig. 3). The size of the larval protegulum in *Apheoorthina* aff. *ferrigena* (420 µm wide and 210 µm long) falls within the range of other plectorthoids, in particular that of *Ocnerorthis* (280–520 µm), up to now the only genus of the family Eoorthidae in which the protegulum has been identified and measured (Freeman and Lundelius 2005). The size of protegulum along with the presence of a small embryonic region surrounded by a larger larval region strongly suggest that *A.* aff. *ferrigena* had planktotrophic larvae.

Faunal affinities of the Early Ordovician Central Andean brachiopods.—The only known late Cambrian (Furongian) rhynchonelliform brachiopods from the Central Andean Basin are *Protorthisina simplex* Benedetto, 2007b and *Finkelnburgia samensis* Kobayashi, 1937, the generic status of the latter pending revision (similar material from NW Argentina was referred to *Apheoorthis* sp. by Ulrich and Cooper 1938).

The Tremadocian has yielded the following genera (Table 1): *Chaniella* Benedetto, 2009, *Astraborthis* Williams, 1974, *Notorthisina* Havlíček and Branisa, 1980, *Kvania* Havlíček, 1994, *Lesserorthis* Benedetto, 2007b, *Gondwanorthis* Benedetto and Muñoz, 2016, *Lampazarorthis* Benedetto and Muñoz, 2016, *Tarfaya* Havlíček, 1971, *Lipanorthis* Benedetto (in Benedetto and Carrasco, 2002), and *Apheoorthina* Havlíček, 1949 (Havlíček and Branisa 1980; Benedetto and Carrasco 2002; Benedetto 2007b, 2009; Villas et al. 2009; Benedetto and Muñoz 2016; this paper). Among them, *Chaniella*, *Notorthisina*, and *Kvania* are of early Tremadocian age, while the remaining are late Tremadocian. It should be noted that the genus *Nanorthis*, to which most of the Tremadocian rhynchonelliforms from the Central Andean Basin had been previously referred, is not represented in this basin (Villas and Herrera 2004; Benedetto and Muñoz 2016; Muñoz 2016). On the other hand, the genus *Riograndella* Kobayashi, 1937 (type species *Riograndella subcircus* Kobayashi, 1937) should be regarded as nomen dubium because neither description nor illustrations are good enough

Fig. 2. Eoorthid brachiopods *Apheoorthina* from Bohemia and Argentina. **A**. *Apheoorthina ferrigena* Havlíček, 1949; Třenice Formation, lenses of haematite from mine near Holoubkov, Prague Basin, Czech Republic; Tremadocian (from Havlíček 1977: pl. 4: 12). NML 9982, exterior of dorsal valve. **B**–**M**. *Apheoorthina* aff. *ferrigena* Havlíček, 1949; Santa Rosita Formation, road from Santa Victoria to Acoyte, Salta Province, NW Argentina; upper →

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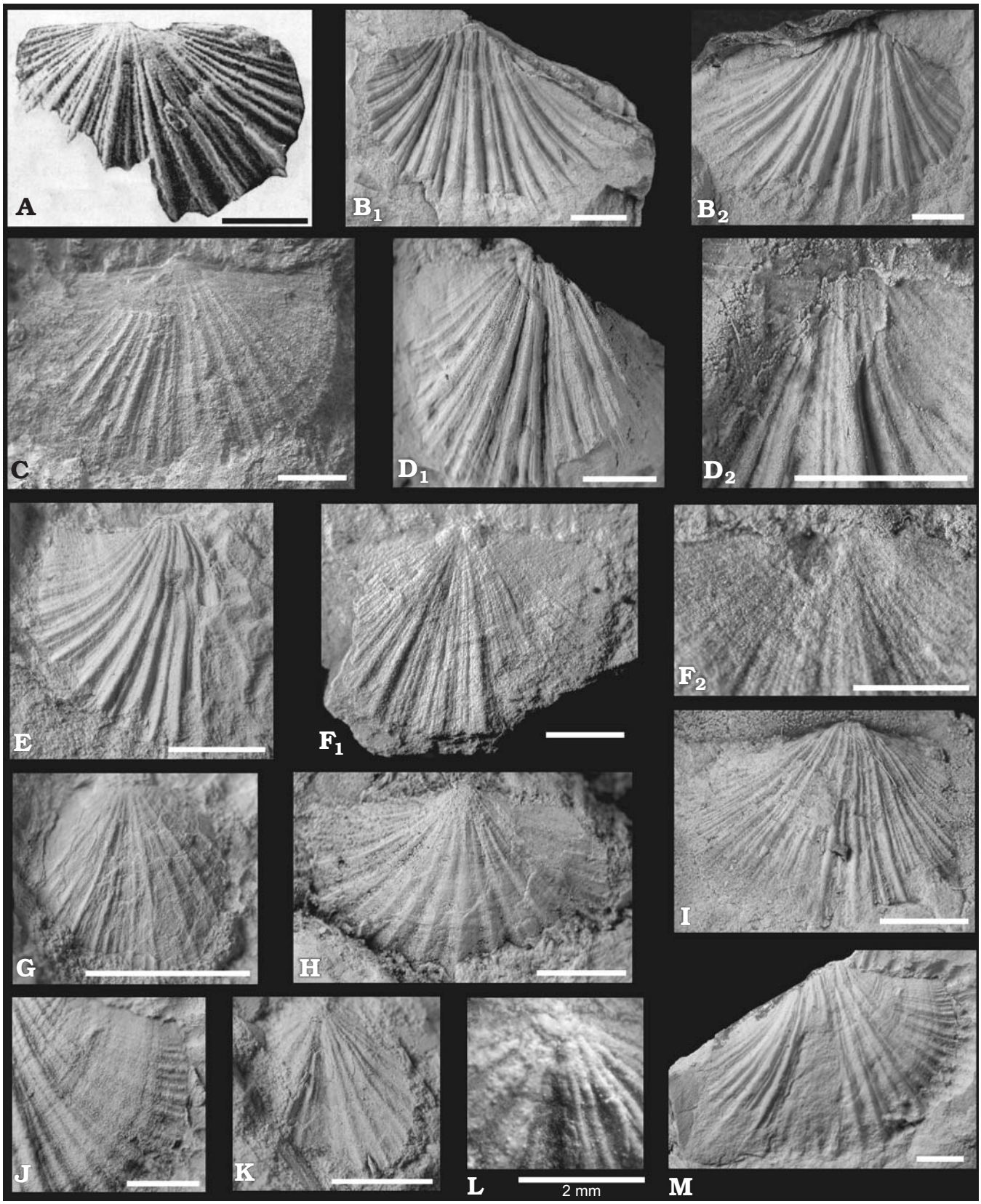

Tremadocian. **B**. CEGH-UNC 26596, dorsal external mould (B_1) and latex cast (B_2). **C**. CEGH-UNC 26597a, dorsal internal mould. **D**. CEGH-UNC 26599, ventral internal mould. **E**. CEGH-UNC 26598, ventral internal mould (E_1) and latex cast (E_2). **F**. CEGH-UNC 25697a, dorsal internal mould (F_1) and detail of cardinalia, latex cast (F_2). **G**. CEGH-UNC 26915, fragmentary dorsal exterior. **H**. CEGH-UNC 26603, ventral exterior. **I**. CEGH-UNC 26916, dorsal exterior (latex cast). **J**. CEGH-UNC 26917, ventral exterior, detail of ornamentation. **K**. CEGH-UNC 26601, dorsal exterior. **L**. CEGH-UNC 26918, dorsal exterior showing protegulum. **M**. CEGH-UNC 26600, exterior of dorsal valve. Scale bar 3 mm, unless otherwise noted.

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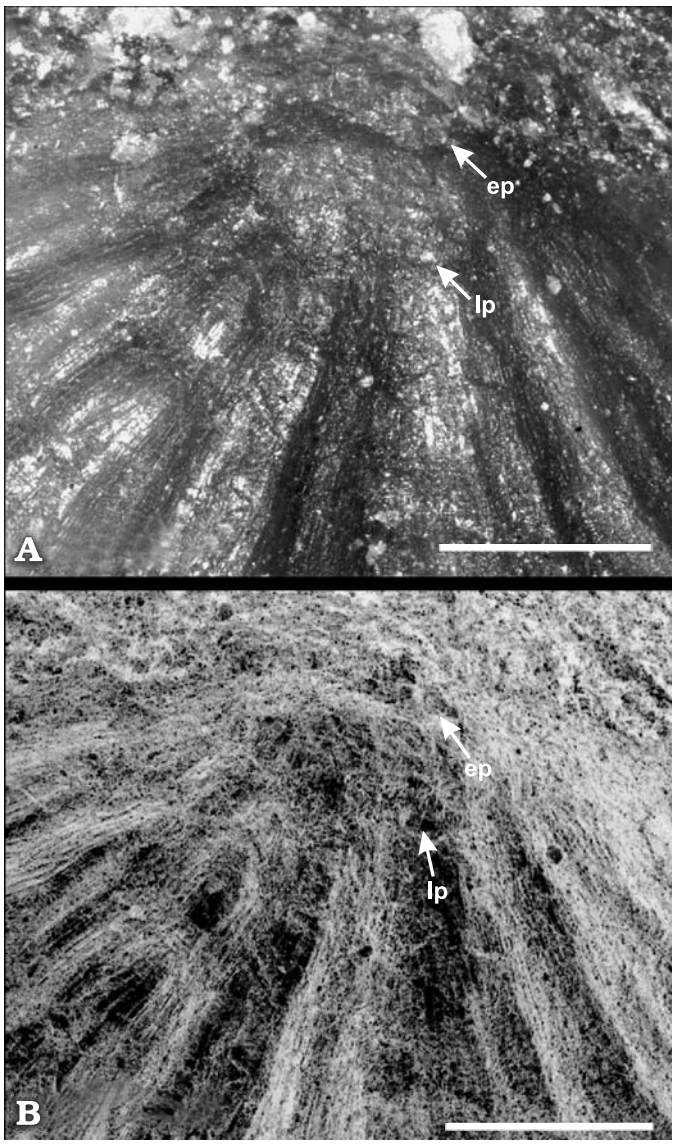

Fig. 3. Eoorthid brachiopod *Apheoorthina* aff. *ferrigena* (Havlíček, 1949), CEGH-UNC 26918, upper Tremadocian, road from Santa Victoria to Acoyte, Salta Province, NW Argentina. Dorsal valve (illustrated on Fig. 2L) showing detail of embrionary (ep) and larval protegulum (lp). High-resolution confocal laser scanning microscopy positive image (**A**) and negative image (**B**). Scale bar 400 µm.

to identify this genus. Furthermore, the type material, whose location remains unknown, is from an isolated boulder of uncertain age found in the Río Grande river bed, probably near the Jujuy city in NW Argentina (not from Bolivia as mentioned in the *Treatise* [Williams and Harper 2000]).

Early Ordovician linguliform brachiopods from the Central Andean Basin are still poorly known. Majority of the taxa described by Harrington (1937, 1938) need revision and are not suitable for biogeographic analysis. On the other hand, acrotretids and siphonotretids, though abundant, are currently under study. Benedetto and Muñoz (2015) described a Bohemian-type lingulacean assemblage from the Tremadocian of NW Argentina which includes *Ectenoglossa*, *Libecoviella*, *Leptembolon*, and the endemic obolid *Torobolus*. *Libecoviella* is typical of Bohemia but recorded also in the Canning Basin of Australia (Brock and Holmer 2004), whereas *Leptembolon* occurs in the Central Andean Basin (Benedetto and Muñoz 2015), Bohemia (Mergl 2002), Baltica, and Southern Urals (Popov and Holmer 1994). The latter is a conspicuous component of the peri-Gondwanan *Thysanotos-Leptembolon* Association (Popov and Holmer 1994; Bassett et al. 1999). Recently, Mergl et al. (2015) recorded a late Cambrian lingulate assemblage from the lower part of the Santa Victoria Group of NW Argentina including the new elkaniid *Saltaia* and new species of ?*Lingulella*, *Libecoviella*, *Eurytreta*, and *Schizambon*. However, the association of this fauna with abundant specimens of the plectorthoid *Gondwanorthis calderensis* (Benedetto, 2007b) (= *Nanorthis calderensis*) cast doubts on its Furongian age because this species is confined throughout the basin to the lower Tremadocian *Cordylodus angulatus* Conodont Zone (Benedetto 2007b; Villas et al. 2009; Benedetto and Muñoz 2016). In any case, the record of *Libecoviella* in the Furongian–lower Tremadocian is the oldest presently known, suggesting an origin and early diversification of the genus in the Central Andean Basin and its subsequent migration along the margins of Gondwana. *Eurytreta* is a widespread taxon recorded in Laurentia, Chu-Ili, and Chingiz Kazakhstanian terranes (Popov and Holmer 1994), South Urals, and east Avalonia (Sutton et al. 2000). It is interesting to note the presence of *Eurytreta* in the nearly coeval Tiñu Formation of the Mexican Oaxaquia terrane (Streng et al. 2011), which by the Cambrian–Ordovician transition lay at southern-temperate latitudes close to the Amazonian margin of Gondwana (Fig. 4) (Keppie et al. 2008 and references therein). The siphonotretid *Schizambon* had a near cosmopolitan distribution preferably inhabiting tropical and temperate waters (Laurentia, Kazakhstanian terranes, west Antarctica, Estonia, Altai), but also having been recorded in the Montaigne Noire (France) (González-Gómez 2005), which was part of the subpolar Armorican Terrane Assemblage (ATA) sensu Cocks and Torsvik (2006).

A significant faunal turnover took place in the early Floian (*Tetragraptus akhzarensis–Baltograptus deflexus* biozones). As in the Tremadocian, the Andean assemblages were dominated by orthides (Havlíček and Branisa 1980; Benedetto 1998a, 2001; Villas and Herrera 2004; Gutiérrez-Marco and Villas 2007) of which *Tarfaya*, ?*Tissintia*, *Euorthisina*, *Incorthis*, and *Lipanorthis* are thought to have originated from local Tremadocian ancestors (Benedetto and Muñoz 2016), whereas *Desmorthis*, *Glyptorthis*, *Hesperonomia*, *Paralenorthis*, and *Camerella* are widespread forms that probably migrated into the basin from low-latitude shelves. The presence of *Monorthis* and ?*Mollesella* in upper Floian strata of the Chilean portion of the Central Andean Basin (Benedetto et al. 2008), and the record of *Ahtiella* in the Floian of Perú (Gutiérrez-Marco and Villas 2007), Bolivia (described as *Valcourea* sp. by Havlíček and Branisa 1980: pl. 2: 7), and Famatina Range of western Argentina (Benedetto et al. 2003), indicate a link not only with the

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volcaniclastic successions of the Famatina-Puna volcanic arc but also with Avalonia, where *Ahtiella* is associated with brachiopods of Celtic biogeographic signature (Neuman 1984), and with Baltica. Although *Ahtiella* is very common in the Darriwilian limestone of the Precordillera terrane, its brachiopods clearly differ from the Andean faunas in its higher taxonomic diversity, the remarkable abundance of pentamerides and strophomenides (Benedetto 2001, 2007a), and in having a mixed Baltic, Celtic, and Laurentian biogeographic signature (Herrera and Benedetto 1991, Benedetto 1998b). *Euorthisina* has been recorded in Floian strata of the Andean region (Peru, Bolivia, Argentina) and South China (Zhan et al. 2006), and in the Darriwilian of North Africa and the Prague Basin (Havlíček et al. 1994). *Gondwanorthis*, one of the most typical brachiopods of the Andean Tremadocian, is known from coeval strata of Iran (Lut terrane) (Ghobadi Pour et al. 2011). *Tarfaya*, a very common genus in the upper Tremadocian–lower Floian of the Andean basin, is also present in northern Africa (Havlíček 1971) and Iran (Popov et al. 2009). *Lipanorthis* sp. was reported by Reyes-Abril et al. (2011) from the Darriwilian of the Central-Iberian Zone of Central Spain. *Incorthis* occurs in the Central Andes and NW Africa (Mergl 1988), the biogeographical link between these regions being stressed by the presence in NW Argentina of a species close to the Moroccan *I. marocana* Mergl, 1988 (Benedetto 1998a).

In brief, nine out of the fourteen brachiopod genera occurring in the Tremadocian of the Central Andean Basin (~64%) are shared with one or more Mediterranean sites (including Iran), four of which (~28%) have been recorded in the Prague Basin, and two (*Kvania* and *Apheoorthina*) are exclusive of the Andean and Bohemian regions. The remaining five (~36%) are endemics. In the Floian nine genera have been identified, three of which occur in the Mediterranean region (~33%) (*Euorthisina*, *Lipanorthis*, *Incorthis*), and one (*Ahtiella*) has been recorded in Baltica and Avalonia (Wales, Newfoundland). The remaining are widespread genera lacking specific biogeographic value (*Paralenorthis*, *Glyptorthis*, *Heperonomia*, *Desmorthis*, and *Camerella*).

Dispersal pathways around Gondwana.—Factors controlling dispersal of marine animals in general, and brachiopods in particular, are variable and their relative role is difficult to assess even in living species. Overall, those factors recognized as having major significance for large-scale distribution of brachiopods can be grouped into three categories: (i) environmental/physical factors, (ii) larval capacity for dispersal, (iii) oceanic current patterns (Valentine and Jablonski 1982).

Physical factors: Evidence from present-day brachiopod species indicate that physical factors such as water depth, temperature, and energy do not constrain significantly their geographic distribution, the main limiting factor being their capacity to colonize different kind of substrates (Richardson 1997). Thus, generalist species that are not affected by grain size, composition, and consolidation of the sea bed tend to

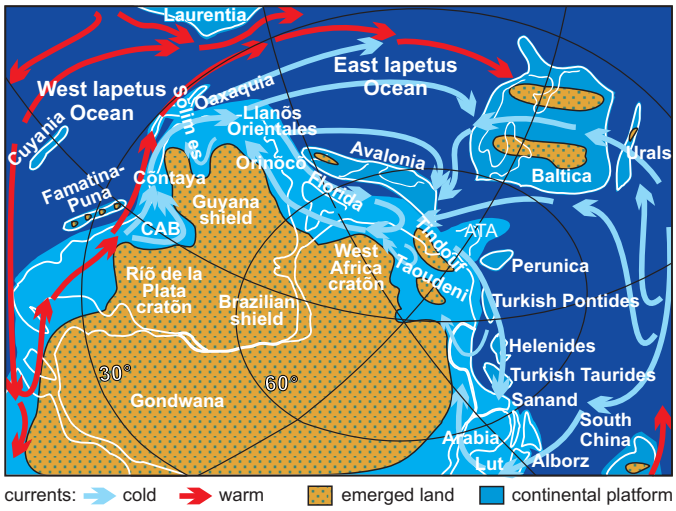

Fig. 4. Early Ordovician palaeogeographic reconstruction showing inferred marine current pattern and possible dispersal routes between the Central Andean Basin, northern Africa, and European-Asian peri-Gondwanan terranes. Considering their position in the Ordovician maps, the names "East" and "West" Iapetus are proposed to replace the commonly used "North" and "South" Iapetus. ATA, Armorican Terrane Assemblage; CAB, Central Andean Basin. Palaeogeography based on Benedetto and Sánchez (1996), Astini (1998), Benedetto (2003), Fortey and Cocks (2003), Ramos (2009), Cocks and Torsvik (2013), and Torsvik and Cocks (2013a, b). Oceanic current pattern based on Pohl et al. (2015).

have wider distributions than those attuned to specific substrates. In the lower Palaeozoic, however, when taxonomic/morphologic diversity was much higher than today, there was a latitudinal segregation at the level of higher taxa, i.e., pentamerides were common in the tropical and subtropical carbonate platforms whereas orthides dominated in the mid- to high-latitude clastic shelves (Benedetto 2001). On the basis of the varied types of sediment in which representatives of *Apheoorthina* aff. *ferrigena* have been found (shoreface shell concentrations, rough-water consolidated ferruginous sandstone, silty/muddy platform sediments deposited below fair-weather wave base) we can speculate that it was a generalist species capable of colonizing different kind of substrates and consequently able to move along the continental shelf and nearshore waters marginal to Gondwana.

Larval dispersal: Transport of larvae of benthic organisms by marine surface currents has been studied in detail by Scheltema (1977, 1986). It should be noted that the terms "transport" and "dispersal" are not equivalent. As they have been redefined by Pineda et al. (2007); transport means the horizontal displacement between two points, whereas dispersal refers to the spread of larvae from a spawning source to a settlement site. Although patterns of water circulation are far from linear (often forming meanders and eddies) and varying seasonally, displacement of larvae take place essentially along the shore. Ecological barriers, such as estuaries, or topographic obstructions, do not prevent dispersal, the main constraint being the direction and velocity of currents (present-day currents range 0.5–2 km/h) and the duration of the pelagic larval life. Transcontinental dispersal (e.g.,

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from North America to Europe) may occur when larvae are carried out by the major wind-driven circulation gyres (e.g., North Atlantic Gyre). It should be noted that most of larvae are transported along the continents by strong boundary currents (e.g., Gulf Stream) and do not cross directly the open oceans whose surface waters tend to be relatively static and have lower nutrient concentration than platform waters (Dore et al. 2008).

As discussed before, it is inferred that *Apheoorthina* possessed long-lived planktotrophic larvae. Duration of pelagic stage in Palaeozoic brachiopods remains speculative. It has been inferred mostly from comparison to present-day lingulids and craniids having planktotrophic larvae in the water column for four to six weeks prior to the settlement depending on the species and environmental factors such as water temperature, food availability, and location of a suitable substrate (Williams et al. 1997). According to Kauffman (1975), dispersal along continuous platforms marginal to large continents took place episodically by successive colonization of new populations. Since a continuous gene flow between geographically separated populations is maintained, allopatric speciation is unlikely to occur (Scheltema 1977). This could be the case of *Apheoorthina*, which seems to be represented by the same species in Bohemia and South America. Although in the Třenice Formation biostratigraphically significant fossils are lacking, available evidence suggests a mid Tremadocian age (Mergl et al. 2007) and consequently the record of *Apheoorthina* in the Prague Basin is slightly older than in Argentina. This led to the inference that *Apheoorthina* originated in Perunica, presumably as an immigrant from the syntrophioidean/eoorthid-dominated associations inhabiting the late Cambrian–Tremadocian low-latitude platforms (Bassett et al. 2002). The phylogenetic analysis of Andean plectorthoideans carried out by Benedetto and Muñoz (2016: fig. 9) indicates that members of the *Protorthisina–Kvania–Gondwanorthis–Tarfaya* lineage originated and diversified in the Andean Basin; therefore the dominant sense of migration was eastwards, from the Central Andean Basin towards North Gondwana (Benedetto 2007b; Fatka and Mergl 2009). The same direction is indicated by the record of *Ahtiella* in the Floian of Peru and Famatina Range, which predates the Dapingian–lower Darriwilian occurrences in Avalonia (Wales, Newfoundland), Cuyania, and Baltica (Gutiérrez-Marco and Villas 2007: fig. 8). Also, the inferred origin of *Euorthisina* from the late Tremadocian *Notorthisina* (Benedetto and Muñoz 2016), so far restricted to the Central Andean Basin (Peru, Bolivia, NW Argentina), supports dispersal along the Gondwana margin from temperate to polar latitudes. Finally, the above-mentioned recent discovery of *Libecoviella* in the uppermost Cambrian–lower Tremadocian of NW Argentina (Mergl et al. 2015) adds further weight to a transport direction from the proto-Andean to the Mediterranean margin of Gondwana.

Oceanic current patterns: To reconstruct the possible dispersion pathways connecting the Andean region with North Africa and the European peri-Gondwanan terranes we have to take into account (i) the configuration of the pre-Andean continental margin and (ii) the Early Ordovician ocean-surface circulation. There is general agreement that the Andean region was a part of the vast Neoproterozoic–Palaeozoic Terra Australis accretional orogen (Cawood 2005). Although its physiography was not uniform across a north-south transect (present coordinates), the typical scenario was that of a more or less continuous belt of volcanic islands (the Famatina-Puna belt) surrounded by narrow platforms. The magmatic arc was generated by subduction of the East Iapetus oceanic plate under Gondwana continental crust (Benedetto 1998b, 2004; Astini 1999, 2003). The presence of some microcontinents (e.g., Paracas, Oaxaquia, Cuyania) approaching/colliding at different times through the lower Palaeozoic adds further complexity to the pre-Andean margin geography (Ramos 2009 and references therein). On the adjacent continental plate extensive back-arc/foreland basins developed (the "South American Pericraton" of Erdtmann 1996). The sea penetrated deeply into the continent, generating several hundred kilometers wide epicontinental embayments filled by clastic sediments derived both from the orogenic belt and the Brazilian craton (Astini 2003; Astini and Marengo 2006). The Central Andean Basin continues "northward" (poleward in the Ordovician geography) into the Contaya Basin in east-central Peru and farther north in the subsurface of the Solimões basin of western Brazil (Wanderley Filho et al. 2007). In SE Colombia, *Cruziana*-rich reddish conglomerate and sandstone of Lower Ordovician age crop out near the Guyana shield margin (Théry et al. 1984). The Ordovician marine sedimentary cover culminates in the northern corner of South America with widespread clastic rocks lying in the subsurface of the Colombian and Venezuelan pre-Andean plains ("Llanos Orientales") and in the eastern Venezuelan Orinoco plains (Ulloa et al. 1982; Benedetto and Ramírez Puig 1982; Mojica and Villarroel 1990). Black shales of Furongian–Tremadocian age form small exposures at El Baúl Massif in central Venezuela. These clastic platforms could have been connected to the east with the West African craton which was flooded since the Cambrian by a broad epicontinental sea. Ordovician deposits accumulated mainly into the Taoudeni and Tindouf basins, the latter superbly exposed in the Moroccan Anti-Atlas Mountains. The African successions were probably continuous with the Suwanee Basin lying in the subsurface of the Florida Peninsula, which is widely accepted that before its accretion to Laurentia occupied the gap between NE South America and NW Africa (Pojeta et al. 1976; Villeneuve 2005; Guiraud et al. 2005; Mueller et al. 2013). The North African transgression can be traced eastwards into the NW Arabian Peninsula, Turkey, and the complex of Asian suspect terranes (e.g., Lut, Sanand, Alborz, Taurides, and Afghan; Cocks and Torsvik 2002; Fortey and Cocks 2003; Fig. 4). The Lut Terrane (Central Iran) appears to have been located marginal to NE Africa (present coordinates) forming the passive margin of Gondwana (Torsvik and Cocks 2013a, b), which continued eastwards to

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north-eastern India (Lhasa and Qiangtang Tibetan terranes). A short distance off the Afghan-Indian sector of Gondwana lay the combined Annamia-South China continent (Torsvik and Cocks 2009; Cocks and Torsvik 2013).

It is widely known that surface oceanic circulation patterns regulate the distribution of benthic organisms in defining preferential migration pathways. In turn, the configuration and distribution of continents is the primary control on the oceanic surface circulation in establishing major physical barriers. Conceptual models of lower Palaeozoic global oceanic circulation based mainly on the fundamental laws of physical oceanography were presented by Wilde (1991), Christiansen and Stouge (1999a, b), and Servais et al. (2014). Numerical models by Poussart et al. (1999) and Herrmann et al. (2004) essentially support the Wilde (1991) conceptual model. A new set of ocean circulation simulations for the Ordovician Period produced by the coupled ocean-atmosphere general circulation model were constructed by Pohl et al. (2015). These models, besides the palaeogeographic configuration, take into account the sensitivity of the circulation pattern to the atmospheric pCO_2. We chose for our analysis the simulation assuming intermediate (8 PAL) CO_2 levels, which is more consistent with the brachiopod distribution. The general circulation pattern for 480 Ma was simplified and redrawn for the area relevant to this paper (Fig. 4). The map shows that the Central Andean margin was dominated by the cold-water Antarctica Current (approximately equivalent to the South Polar Current of Wilde 1991), which merges with the Southern Westerlies current forming the southern component of the anticlockwise East Iapetus Gyre. Along the northern margin of Gondwana the circulation pattern centred at about 60° S was dominated by the clockwise Rheic Gyre. Despite the complex non-zonal pattern produced by multiple current deflections around the peri-Gondwanan landmasses, the general sense of circulation was eastwards. This favoured a more or less continuous faunal dispersion from the Andean basins to North Africa, Avalonia, Armorica Terrane Assemblage, and Perunica, reaching eastwards the Arabian Peninsula, the Iranian terranes and the South China palaeocontinent. On the other hand, the Gondwana Current flowing to the south of the Rheic Gyre would have connected the water masses of North Africa with the epicontinental seas of South America, which could explain the reversed migration of some brachiopods from the north Gondwanan terranes to the Andean region.

The Famatina-Puna volcanic arc, located at ca. 30° S off the proto-Andean margin in the West Iapetus Ocean (Fig. 4), could have been influenced by the southern limb of the warm-water anticlockwise South Panthalassic Gyre (Pohl et al. 2015: fig. 4b). This may account for the presence in the Floian of western Puna of several pentamerides and clitambonitoideans which are unusual in the Central Andean Basin but are distinctive for the more temperate waters of the Famatina basin and especially the warm-water Cuyania platform limestone (Benedetto 2001). The same current may have established limited communication with the Central Andean epicontinental sea and presumably was responsible for the exchange between the Famatina-Puna volcanic arc and the volcanic islands within the East Iapetus Ocean bearing Celtic brachiopods.

Conclusions

A species closely comparable to *Apheoorthina ferrigena* Havlíček, 1949 from the Třenice Formation of the Prague Basin is reported from upper Tremadocian strata of northwestern Argentina. This is the first record of *Apheoorthina* outside the Bohemian region strengthening its faunal affinities with the Central Andean Basin of South America. Although global data of Tremadocian brachiopods are still too limited for quantitative analyses of faunal affinities, available evidence indicates that the Central Andean Basin shares with the Mediterranean region about two-thirds of brachiopod genera, and that nearly one-third of them are present in the Prague Basin. According to the size of protegulum and the presence of a small embryonic region surrounded by a larger larval region we infer that *A.* aff. *ferrigena* possessed long-lived planktotrophic larvae. Moreover, as this species has been recorded in different lithofacies, we speculate that it was a generalist form capable of colonizing a wide range of substrates and environmental settings. Phylogenetic and chronologic evidence indicate that brachiopod dispersal was mainly from the Andean region towards North Gondwana. According to recent Early Ordovician conceptual models of ocean-surface circulation the Central Andean continental margin was dominated by the cold-water Antarctica current which merged with the Southern Westerlies current forming the southern component of the anticlockwise East Iapetus Gyre. This current pattern could explain larvae transport from the Andean basins to North Africa, Avalonia, Armorican Terrane Assemblage, and Perunica, reaching eastwards the Arabian Peninsula and the Iranian terranes. In turn, the Gondwana Current flowing to the south of the Rheic Gyre would have connected the epicontinental seas of North Africa and western South America (present coordinates) accounting for the reversed migration sense of some brachiopods.

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