

Original Article

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Author for correspondence:

Leonid E. Popov,
Email: lepbarry@yahoo.co.uk

The identity and significance of the high-latitude Early Ordovician Mediterranean brachiopod Province

L. Robin M. Cocks¹ and Leonid E. Popov² 

¹Department of Earth Sciences, The Natural History Museum, Cromwell Road, London SW7 5BD, UK and ²National Museum of Wales, Cathays Park, Cardiff CF10 3NP, UK

Abstract

During the Early Ordovician Epoch, the Mediterranean brachiopod Province was extensive in the higher-latitude sectors of the globe in the Southern Hemisphere. The latter was much occupied by the massive continent of Gondwana, which stretched from north of the Equator S-wards to cover the South Pole. The Mediterranean Province can be separated into two groups: Group 1, the higher-latitude fauna dominated by large linguliform brachiopods; and Group 2, which is more diverse, particularly in orthides. The large linguliform brachiopod faunas are particularly well known in southern Europe (France, Spain and Bohemia) and North Africa, and the second group in Avalonia, Chile and Argentina. The province is different from, but merges with, more diverse contemporary faunas in the lower latitudes of Gondwana to its north, although the latter contrast with other lower-latitude faunal provinces in South China, Laurentia, Siberia and elsewhere. Since the Rheic Ocean between Avalonia and Gondwana was relatively narrow during the Early Ordovician Epoch, the Avalonian brachiopods were integral parts of the Mediterranean Province, but only until end of the Dapingian Age. This paper focuses on the earlier phases of the Mediterranean Province, although the province continued until near the end of the Ordovician Period. Intermediate-latitude Baltica and some other faunas are included in new principal components and other analyses in order to compare them with the Mediterranean Province faunas. Radiation was very significant for many brachiopod taxa during the period, with first appearances of the Plectambonitoidea (Taffiidae), several orthide families (Euorthisinidae, Tarfayidae and Anamalorthidae) and the earliest endopunctate orthide, the dalmanelloid *Lipanorthis*.

1. Introduction

It is now generally appreciated that the Palaeozoic biodiversification of invertebrate animals did not just peak in the radiations of early Cambrian time (the Cambrian Explosion) and during the Ordovician Period, the Great Ordovician Biodiversification Event of Webby *et al.* (2004), but proceeded reasonably steadily from early Cambrian time up to near the end of the Ordovician Period (Harper *et al.* 2020). During the Early Ordovician Epoch, the major continents were well separated by substantial oceans (Fig. 1), and that allowed the development of several distinct faunal provinces, as reviewed by Fortey & Cocks (2003). It also meant that the radiation rates differed between the different major areas at different times; for example, the curves shown by Fan *et al.* (2020), based largely on Chinese data, have highs and lows at different times from those shown in Harper & Servais (2013), which gathered data from all parts of the world. Nevertheless it is clear that the number of brachiopod genera approximately doubled between the beginning of the Ordovician Period and the end of the Dapingian Age only 20 Ma later.

The best known of those benthic faunas from the higher latitudes are chiefly brachiopods and trilobites, and the latter made up a calymenacean–dalmanitacean (formerly *Neseuretus*) Province in the Early Ordovician Epoch (Cocks & Fortey, 1990; Fortey & Cocks, 2003). The brachiopods were largely within the Mediterranean Province, and the chief aim of this paper is to reidentify those Mediterranean faunas, to compare the individual sites statistically to gain a more nuanced overall picture of the integrity of the province, and to see how the assemblages that make up the province changed from the early Tremadocian Age to the end of the Dapingian Age (during 487–469 Ma). We have also revised some of the contemporary benthic brachiopod faunas on the neighbouring continent of Baltica, whose centre drifted speedily from 45° S to 30° S during that period (Torsvik & Cocks, 2017), in order to compare and contrast that Baltic Province and its changes with the Mediterranean Province.

The Mediterranean Province is only known from the higher southern latitudes of the world since the comparable high latitudes surrounding the North Pole were entirely covered by the very extensive Panthalassic Ocean; any possible land areas, and therefore their surrounding benthic faunas within it, are quite unknown. The Province continued on into later

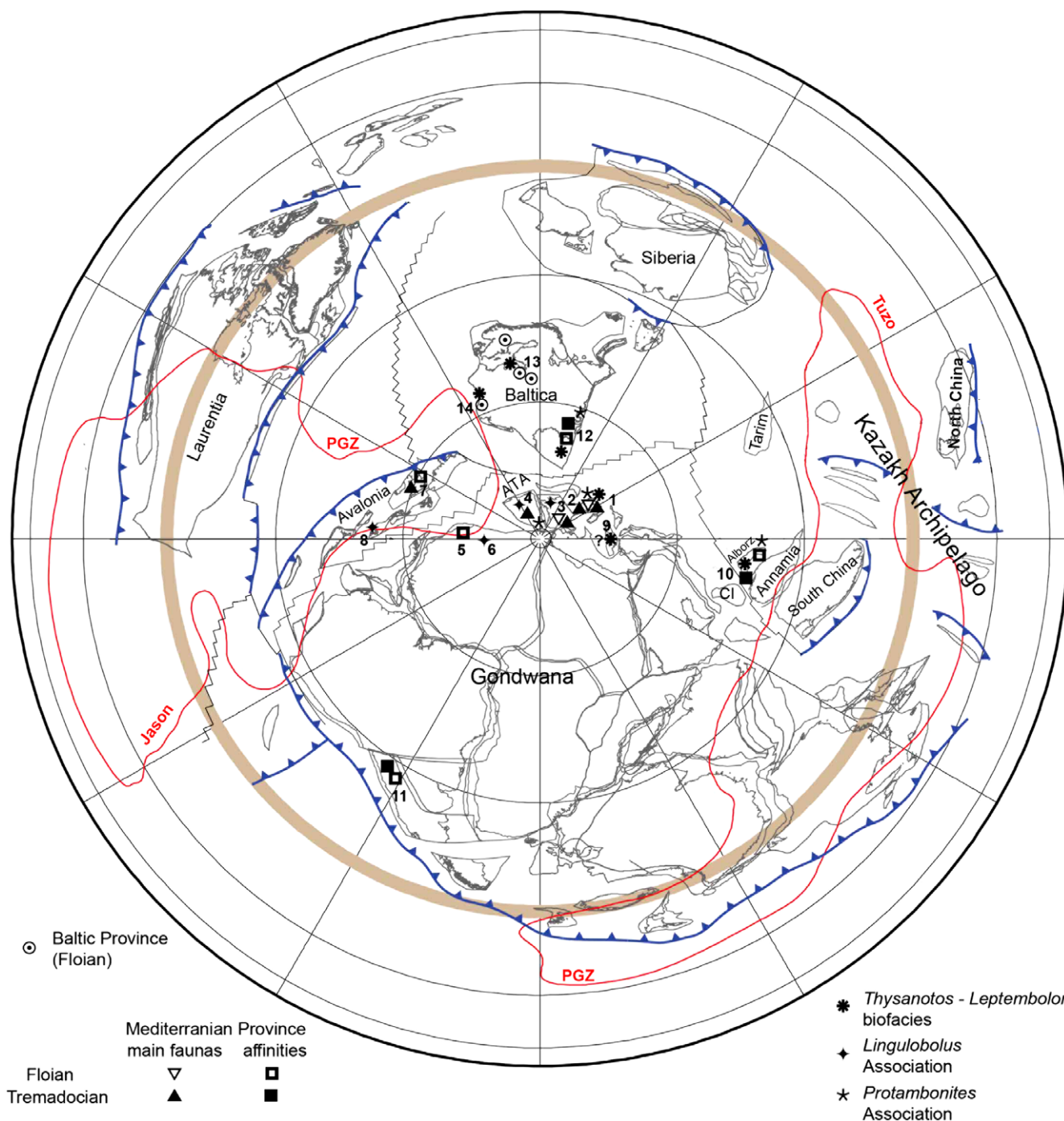


Fig. 1. (Colour online) Palaeogeography of Gondwana during Early Ordovician time (480 Ma), showing the chief brachiopod localities within the higher latitudes analysed in this paper. Base map modified from Cocks & Torsvik (2020). 1, Bohemia; 2, Moldanubia; 3, Armorica; 4, Iberia; 5, 6, NE Africa (Ougarta Range, Anti-Atlas Mountains); 7, East Avalonia; 8, West Avalonia (Acadia); 9, Serbia; 10, Alborz-Kopet-Dagh; 11, Central Andean Basin (Colorado); 12–14, Baltica continent; 12, South Urals; 13, Ingria, Russia and North Estonia; 14, Holy Cross Mountains, Poland; ATA, Armorican Terrane Assemblage; CI, northeastern central Iran platform; PGZ (and red lines), Jason and Tuzo plume generation zones.

Ordovician time (late Darriwilian – early Katian) with other characteristic but different brachiopod genera, such as *Tissintia*, but that later history is not considered in detail here.

Spjeldnaes (1961) originally introduced the term ‘Mediterranean Province’ for a distinctive cooler Ordovician climatic zone, a concept that pre-dated the awareness of plate tectonics. However, later authors (e.g. Havlíček & Vaněk, 1966) used it as the name of a faunal province, which we follow here, although the Mediterranean Province was called the ‘High-latitude Province’ by Harper *et al.* (2013).

The Early Ordovician Epoch of previous general usage included the Tremadoc and Arenig ages, but the Tremadoc is now known as the Tremadocian Age and the Arenig has now been replaced by the Floian, Dapingian and earliest part of the Darriwilian ages in the international system of stratigraphical nomenclature (Bergström *et al.* 2009).

The faunas analysed here date from the Tremadocian, Floian and Dapingian ages, and their sample identifying letters (e.g. B1) are to be found in the rest of this paper as well as in

Tables 1–3 and Figures 2, 3. The relevant areas and their brachiopods are now briefly reviewed in turn.

2. Gondwana

The largest continent by far during the Early Ordovician Epoch was Gondwana, which stretched from north of the Equator Swards to cover the South Pole, which was then under North Africa (Fig. 1). Because it covered so many latitudes, there were biogeographical clines at Gondwana's eastern and western margins (Cocks & Fortey, 1988). In the sector of Gondwana that straddled the Equator to both the north and south, there were the dikelokephalinid trilobite Province and the Cathay-Tasman brachiopod Province (Cocks & Torsvik, 2020), while in the medium to higher latitudes there were the intermediate-latitude brachiopod provinces (including Baltica) as well as the Mediterranean Province discussed here.

The Cambrian origins of the Mediterranean brachiopod faunas are obscured by the significant stratigraphical gaps caused by global late Cambrian – Early Ordovician regressions, which resulted in condensed intervals and erosive unconformities in the Anti-Atlas Mountains of Morocco, the Cantabrian Zone and SW Sardinia (both then within Iberia), and the southern Montagne Noire of France, while the Armorican Massif completely lacks rocks of late Cambrian (Furongian) and Early Ordovician (Tremadocian) ages (Álvaro *et al.* 2007). Extensive Furongian gaps are also documented from Bohemia, the Turkish Taurides (Dean, 2005) and the Uralian margin of the continent of Baltica (Popov & Holmer, 1994). Baltica was separated by only a narrow ocean from the Mediterranean Province sector of Gondwana at the start of the Ordovician Period, although it subsequently drifted rapidly N-wards so that part of it straddled the Equator by the end of the Ordovician Period (Torsvik & Cocks, 2017). There are relatively continuous late Cambrian (Furongian) successions in the southern Montagne Noire and the Iberian Chains (Álvaro *et al.* 2007), yet only two rhynchonelliform genera (*Billingsella* and *Saccogonum*) are documented from there (Havliček & Josopait, 1972). Although Cambrian linguliforms were represented by the moderately rich micromorphic brachiopod assemblage near the Guzhangian–Furongian boundary interval, there is no sign of the large shallower-water lingulide biofacies in Gondwana until after the end of the Tremadocian Age. Many of those faunas also lack any orthides, which are usually one of the main components of the Early Ordovician Mediterranean Province.

Hiatuses and highly condensed sedimentation are also characteristic of the Dapingian – early Darriwilian time interval in the Mediterranean and Arabian sectors of Gondwana (Videt *et al.* 2010; Ghavidel-Syooki *et al.* 2014; Gutiérrez-Marco *et al.* 2014). As a result, available data on the Dapingian brachiopod taxonomic composition and community structure makes detailed biogeographical analysis very difficult. However, some Dapingian faunas that we have included in this analysis are helpful for observing major trends in the developing biogeographical differentiation of the brachiopod faunas on the moving continents.

3. Armorican Terrane Assemblage

The Mediterranean Province was initially conceived from faunas within the Armorican Terrane Assemblage (Fig. 1, localities 1–4) that surrounds much of the northwestern Mediterranean Sea today (hence the name of the province). Because of later tectonics, chiefly

during the Variscan Orogeny, the Ordovician rocks in that Terrane Assemblage today occur in widely separated outcrops. But, as can be seen from Figure 1 and also Franke *et al.* (2017, fig. 10), the various terranes within the Armorican Terrane Assemblage were all integral parts of the main Gondwanan continent at 480 Ma (late Tremadocian). However, rifting between Iberia, Armorica and Bohemia (to the north) and the main part of the Gondwanan continent, as well as Palaeo-Adria, which included Sardinia, Corsica, Adria and Apulia (to the south), caused the start of the opening of the Galicia–Moldanubian Ocean at some time before 460 Ma (late Darriwilian). Nevertheless that ocean did not become significantly wide until after the end of the Ordovician Period, although extensive strike-slip faulting within it moved the northern Armorican terranes some distance laterally to the west. However, that did not prevent those peri-Gondwanan terranes from slowly drifting outside the Mediterranean Province area during Middle Ordovician time; the reason for this was that the South Pole, although it did move slightly, stayed under the NW Africa sector of Gondwana during the entire Ordovician Period (Torsvik & Cocks, 2017). The Armorican Assemblage terranes are now reviewed individually as follows.

3.a. Bohemia

Bohemia today lies mostly within the Czech Republic (Fig. 1, locality 1). Havliček & Vaněk (1966) listed all the faunas then known from the Mílina Formation (late Tremadocian) and the Klabava Formation (Floian and Dapingian). Havliček (1982) and Mergl (1995, 2002) described the lingulides from the same formations, and Havliček (1977) monographed the Orthida from the entire Palaeozoic strata of Bohemia. Havliček *et al.* (1994) postulated that the Barrandian Basin in the centre of Bohemia formed a large part of an independent terrane that they termed Perunica but, after review, Franke *et al.* (2017) established that during Early Ordovician time it was in the same large fragment of Gondwana (and subsequently peri-Gondwana) as Iberia and Armorica before the late Palaeozoic Variscan events. The faunas in our analysis, all described by Mergl (2002), Havliček (1977) and Havliček & Vaněk (1966), are from the Třenice Formation (middle Tremadocian, B1), the Mílina Formation (upper Tremadocian, B2) and the Klabava Formation (Floian–Dapingian, B3).

A small late Tremadocian – Floian brachiopod fauna with *Angusticardinia*, *Hesperonomiella*, *Hyperobolus* and *Lingulella* is known from an isolated locality at Železné hory, east Bohemia (Budil *et al.* 2016) (B4). While the age constraints for this assemblage are relatively poor, the presence of *Angusticardinia* and *Hyperobolus* is of considerable interest as a possible biogeographical link with approximately contemporaneous faunas of South Urals.

3.b. Bavaria

The Frankenwald of Bavaria, Germany (Fig. 1, locality 2), formed part of the Moldanubian Terrane during the Ordovician Period. A late Tremadocian fauna from the Vogtendorf Formation (Sdzuy *et al.* 2001) (Ba) contains craniids that can be provisionally assigned to *Deliella*, and the rhynchonelliform brachiopods *Jivinella* sp., *Kvania kvanica* (Mergl, 1984), *Poramborthis vonhorstigi* Sdzuy *et al.* 2001, *Poramborthis cf. klouceki* Havliček, 1949 and *Ranorthis franconica* Sdzuy *et al.* 2001.

Another important early Tremadocian fauna was documented by Sdzuy (1955) from the Leimitz Shale Formation. While its strong biogeographic affinity to the Bohemian faunas is evident

Table 1. Mediterranean Province brachiopod genera of Tremadocian age, which are largely from latitudes of > 70° N and within the Armorican Quartzite facies

Locality and unit	Bohemia		Wales and Welsh Borderland		Vogtendorf Formation, Bavaria	Saint Chinian Formation, France	Cabos Series, Cantabrian Mountains	Iberian Chanes ³	Famatina Basin, Argentina								
	Třenice Formation	Milina Formation	Cressagian Stage ¹	Migeneintian Stage ²					Guayoc Chico Group	Las Vicuñas Formation	Cardonal Formation	Devendeus Formation	Santa Rosita Formation	Floresta Formation	Salta Province ⁴	Saladillo Formation	Coquena Formation
	B1	B2	W1	W2					Ba	MN1	CS	IC	A1	A1	A1	A1	A2
LINGULOIDEA																	
<i>Broeggeria</i>			+			+											
<i>Divobolus</i>			+														+
<i>Elliptoglossa</i>			+														
<i>Elkanisca</i>	+																
<i>Eopaterula</i>																	
<i>Expellobolus</i>	+																
<i>Ferrobolus</i>	+																
<i>Hyperbolus</i>	+																
<i>Leptembolon</i>	+	+												+			
<i>Lebecoviella</i>	+													+			
<i>Lingulella</i>			+	+													
<i>Palaeoglossa</i>																	
<i>Pidiobolus</i>		+															
<i>Rowellella</i>																	
<i>Spondyloglossella</i>						+											
<i>Teneobolus</i>	+	+															
<i>Thysanotos</i>	+	+															
<i>Torobolus</i>													+				
ACROTHELLOIDEA																	
<i>Orbithele</i>	+	+		+													
ACROTRETOIDEA																	
<i>Acrotreta</i>	+	+				+											
<i>Dactylotreta</i>	+	+															
<i>Eurytreta</i>			+	+													
<i>Semitreta</i>			+														
SIPHONOTRETOIDEA																	
<i>Celdobolus</i>		+															
<i>Eosiphonotreta</i>		+															
<i>Siphonobolus</i>		+															
<i>Siphonotretella</i>		+															
PATERINOIDEA																	

(Continued)

Table 2. Mediterranean Province brachiopod genera of Floian and Dapingian (Arenig) ages, which are largely in finer-grained facies from latitudes of 35–70° N

Locality and unit	Wales and Welsh Borderland						Mytton Flags Formation, England	Upper Suri Formation, Argentina	Molles Formation Argentina	Bell Island Group, Newfoundland	Khenegel Aatène Formation, Algeria	Upper Fezouata Formation, Morocco	Budleigh Salterton, Devon	Montagne Noire			
	Železné hory, Bohemia	Klabava Formation, Bohemia	Moridunian, SW Wales ¹	Blaencediw Formation, SW Wales	Pontyfenni Formation	Treiorworth Formation, Anglesey								La Maurerie Formation	Cluse de l'Orb Formation	Foulon Formation	Landeyran Formation
	B4	B3	W3	W4	W5	W6	E1	A3	A4		KA	M	Ar	MN2	MN3		MN4
LINGULOIDEA																	
<i>Glossella</i>								+									
<i>Ectenoglossa</i>													+		+		
<i>Elliptoglossa</i>		+															
<i>Elkania</i>		+															
<i>Elkanisca</i>		+															
<i>Expellobolus</i>		+															
<i>Famatinobolus</i>								+									
<i>Fagusella</i>		+															
<i>Hyperbolus</i>	+																
<i>Leptembolon</i>		+															
<i>Lingulepis</i>													+		+		
<i>Lingulella</i>	+	+															
<i>Lingulobolus</i>										+	+		+		+		
<i>Lithobolus</i>		+															
<i>Monobolina</i>			+			+	+	+									
<i>Mytoella</i>		+															
<i>Palaeoglossa</i>			+	+	+	+	+										
<i>Paldiskites</i>		+															
<i>Paterula</i>		+		+	+		+										
' <i>Pseudobolus</i> '													+				
<i>Rafanoglossa</i>		+						+						+	+	+	+
<i>Rosobolus</i>		+															
<i>Rowellella</i>		+															
<i>Sedlecingula</i>		+												+			+
<i>Spondyloglossella</i>		+															
<i>Tarphyteina</i>			+	+	+												
<i>Teneobolus</i>		+															
<i>Tomasina</i>													+				
<i>Westonia</i>		+												+			
DISCINOIDEA																	
<i>Acrosaccus</i>			+	+													
<i>Eoschizotreta</i>		+															
<i>Schizocrania</i>					+												
<i>Schizotreta</i>						+	+										

(Continued)

Table 2. (Continued)

<i>Trematis</i>			+					
ACROTHELIOIDEA								
<i>Orbithela</i>		+						+
ACROTRETOIDEA								
<i>Acrotreta</i>		+						
<i>Chilcotreta</i>							+	
<i>Dactylotreta</i>		+						
<i>Eoconulus</i>		+						
<i>Mamatia</i>		+						
<i>Numericoma</i>		+						
<i>Pomeraniotreta</i>		+						
SIPHONOTRETOIDEA								
<i>Acanthambonia</i>		+						
<i>Celdobolus</i>		+						
<i>Collarotretella</i>		+						
<i>Eosiphonotreta</i>		+						
<i>Siphonotretella</i>		+						
PATERINOIDEA								
<i>Kolithium</i>		+						
<i>Lacunites</i>		+						
CRANIOIDEA								
<i>Petrocrania</i>		+						
PLECTAMBONITOIDEA								
<i>Ahtiella</i>							+	
<i>Aparthophyla</i>		+	+					+
<i>Inversella (Reinversella)</i>						+		
<i>Taffia</i>						+		
POLYTOECHIOIDEA								
<i>Antigonambonutes</i>		+				+		
<i>Tritoechia</i>		+				+	+	+
PROTORTHOIDEA								
<i>Crossiskenidium</i>							+	
<i>Protoskenidioides</i>						+	+	+
<i>Skenidioides</i>			+			+	+	+
CLITAMBONITOIDEA								
<i>Oslogonites</i>						+	+	
<i>Progonambonites</i>								+
ORTHOIDEA								
<i>Astraborthis</i>		+				+	+	+

(Continued)

Table 2. (Continued)

Locality and unit	Wales and Welsh Borderland														Montagne Noire			
	Železné hory, Bohemia	Klabava Formation, Bohemia	Moridunian, SW Wales ^a	Blaencediw Formation, SW Wales	Pontyfenni Formation	Treiorworth Formation, Anglesey	Mytton Flags Formation, England	Upper Suri Formation, Argentina	Molles Formation, Argentina	Bell Island Group, Newfoundland	Khenegeel Aatène Formation, Algeria	Upper Fezouata Formation, Morocco	Budleigh Salterton, Devon	La Maurerie Formation	Cluse de l'Orb Formation	Foulon Formation	Landeyran Formation	
	B4	B3	W3	W4	W5	W6	E1	A3	A4				Ar	MN2	MN3		MN4	
<i>Ferrax</i>		+																
<i>Hesperonomia</i>						+	+											
<i>Hesperonomiella</i>	+					+												
<i>Monorthis</i>			+						+									
<i>Mollesella</i>								+	+									
<i>Ocothis</i>																	+	
<i>Paralenorthis</i>			+	+		+			+							+	+	
<i>Pleurorthis</i>														+				
<i>Poramborthis</i>		+																
<i>Prantlina</i>		+															+	
<i>Productorthis</i>			+			+			+									
<i>Protohesperonomia</i>		+																
<i>Sinorthis</i>																		
<i>Styxorthis</i>		+																
<i>Suriorthis</i>									+								+	
<i>Treioria</i>						+												
PLECTORTHOIDEA																		
<i>Desmorthis</i>						+	+											
<i>Famatinorthis</i>									+									
<i>Fynnonia</i>			+						+									
<i>Ranorthis</i>		+										+					+	
<i>Rhynchorthis</i>			+	+		+												
<i>Platystrophia</i>						+												
DALMANELLOIDEA																		
<i>Angusticardinia</i>	+											+						
<i>Nereidella</i>		+																
<i>Nocturniella</i>		+																
<i>Paurorthis</i>			+	+		+						+					+	
SYNTROPHIOIDEA																		
<i>Camerella</i>							+											
<i>Diaphelasma</i>						+												
<i>Hesperotrophia</i>				+														
<i>Rectotrophia</i>			+			+												
<i>Rugostrophia</i>						+		+										
<i>Trigonostrophia</i>								+										

^a Aberdaron, Carmarthen, Ogof Hên formations, Trematid Beds; also Mytton Flags Formation.

from the occurrence of *Jivinella?*, *Poramborthis*, *Orbithela* and *Thysanotos*, the generic assessments of the species assigned to *Acrotreta*, *Lingulella*, *Nanorthis* and *Siphonotreta* are questionable and the problem cannot be resolved without access to the original collections. That fauna is therefore not included in the cluster analysis presented in this paper.

3.c. Northern France and SW England

In Normandy and Brittany (Fig. 1, locality 3), brachiopod faunas including the distinctive large lingulides were originally described by Rouault (1850) and revised by various subsequent authors, including Cocks (1993), and some of their sites were plotted by Emig & Gutiérrez-Marco (1997). Similar large lingulides of Floian ages are known from Britain only in SW England, where they are found within the Gorran Quartzite of Cornwall and also as pebbles within the Budleigh Salterton Pebble Beds of Budleigh Salterton, Devonshire; both those English faunas are included within sample Ar.

The Gorran Quartzites are large olisthostrome blocks within Early Devonian mélanges that were transported NW-wards from Armorica during the late Palaeozoic Variscan Orogeny, and a few comparable pebbles have been occasionally found within other Permo-Triassic conglomerates from as far north as near Birmingham, central England. Although all lithologically similar and mostly containing higher-latitude Gondwanan assemblages, those Permo-Triassic pebbles contain brachiopods of four different ages: two Ordovician and two Devonian (Cocks, 1993). All of those pebbles must therefore have been transported fluviially from northwestern France after the Variscan Orogeny was over near the end of the Palaeozoic Era, and when Europe had largely become united (Franke *et al.* 2017). The microcontinent of Avalonia, which included nearly all of England and Wales but not Devonshire and Cornwall (see next section), did not itself host any Group 1 Mediterranean Province brachiopods during Early Ordovician time.

3.d. The Montagne Noire

Much has been published on this very tectonized area near Montpellier in southern France, which includes various fragments of Ordovician rock that were all substantially displaced in Devonian and later times in the Variscan Orogeny (Franke *et al.* 2017). Havlíček (1980) described the large lingulide brachiopods, Mélou (1982) the rhynchonelliform brachiopods and, together with Vizcaíno *et al.* (2001), provided a summary of the Cambrian and Ordovician faunas and sediments. Both Group 1 and Group 2 of the Mediterranean Province are seen in the Montagne Noire. The faunas in our analysis are from the Saint Chinian Formation (Tremadocian, MN1), La Maurerie Formation (Floian, MN2), Cluse de l'Orb Formation (Floian, MN3) and the Landeyran Formation (late Floian, MN4).

3.e. Iberia

The whole Iberian Peninsula (Fig. 1, locality 4) can be divided into at least six terranes (often termed 'zones') whose rocks have been intermingled and affected by many orogenic events from late Precambrian time throughout much of the Phanerozoic Eon. Precisely where each terrane lay (and their individual relationships with all of the others) within the Peri-Gondwanan mélange during the Early Ordovician Epoch is quite uncertain in detail, but their contained faunas indicate that they must all have been parts of the Mediterranean Province region (Gutiérrez-Marco *et al.* 2002). Large linguliform brachiopods of Group 1 have been recorded

from many Spanish localities in the Cantabrian, West Asturia-Leonese (WALZ), Iberian Cordillera and Central Iberian zones by Emig & Gutiérrez-Marco (1997), and by Coke & Gutiérrez-Marco (2001) from the Central Iberian Zones of northern Portugal. The occurrence of *Poramborthis hispanica* Havlíček (*in* Havlíček & Josopait, 1972) in the Iberian Chains (IC) represents the most westerly known occurrence of the family Poramborthisidae within the Mediterranean Province. The only other Tremadocian rhynchonelliform brachiopod is the polytoechioid *Protambonites primigenus* Havlíček, which Villas (1995) documented from the Cabos Series (Tremadocian) in the WALZ area of the Cantabrian Mountains and is included in our analysis (CS).

3.f. Eastern Europe

Gutiérrez-Marco *et al.* (1999) described a fauna from Serbia (Fig. 1, locality 9) and Macedonia that included *Lingulobolus* (which may be an erroneous identification of *Leptembolon*), and what Havlíček (1989) recorded as *Thysanobolus?*, although that is a junior synonym of *Thysanotos* (see Mergl 2002). Gutiérrez-Marco *et al.* (1999) also reviewed other faunas from Serbia that may include some Group 1 large lingulids, although that needs confirmation. If it is true, then those faunas would represent the furthest extent of the Group 1 Mediterranean Province assemblage to the east in Europe, which is within a region that has been very much affected by both the Tertiary Alpine Orogeny as well as the Palaeozoic Variscan Orogeny (Franke *et al.* 2017). However, reassessment of this fauna is difficult since the published identifications are problematic and the photographs are poor, and the specimens recall the *Leptembolon-Thysanotos* fauna rather than being clearly comparable to the large lingulides from the Armorican Quartzite; we therefore exclude this fauna from our analysis. Nevertheless, we speculate that this area was part of the Adria and Tisia Terrane (Units 333 and 367 of Torsvik & Cocks, 2017), which was an integral part of the main Gondwanan continent during the Ordovician Period, situated to the north of the NE Africa sector.

4. Avalonia

Apart from its southwestern tip in Devon and Cornwall (which were parts of Armorica), England and Wales both lay within the relatively small continent of Avalonia during Early Ordovician time (Fig. 1, locality 7). That continent had newly separated from Gondwana just prior to Cambro-Ordovician boundary time, with rifting and the initial opening of the Rheic Ocean at about 490 Ma (Cocks & Fortey 2009). Avalonia extended across today's North Atlantic to include parts of Canada (much of Newfoundland, New Brunswick and Nova Scotia) and the United States of America as far south as Cape Cod, Massachusetts. The Early Ordovician rocks exposed in Carmarthenshire and Pembrokeshire, southwestern Wales, were laid down in a relatively deep-water back-arc basin with many volcanics (Traynor, 1988) on the NW margin of Avalonia, and virtually all of the shelly faunas found in many localities within them have been transported from the nearby shelves and redeposited beneath deeper water. The brachiopods from southwestern Wales were revised by Cocks & Popov (2019), and many of those from the Ogof Hên and Blaencediw formations there are typical Group 2 of the Mediterranean Province. Those in our analysis are the Ogof Hên Formation and 'Trematid Beds' (included in W3) (Moridunian: Floian); Brunel Formation (Whitlandian: Floian) (included in W3); Blaencediw Formation (included in W4) (Whitlandian: Floian);

and the Pontyfenni Formation (Fennian: Dapingian) (included in W5). In addition, Cressagian (Tremadocian) faunas from the Llangynog Inlier, also in Carmarthenshire, and the Harlech Dome in north Wales were included in our analysis (W1).

From the Welsh Borderland of England (Shropshire), Williams (1974) described the Ordovician fauna of the Shelve Inlier, where the Floian Stiperstones Quartzite yielded only a few brachiopods, but the succeeding Mytton Flags was found to carry more brachiopods of Floian–Dapingian ages (Williams, 1974), and are included in our analysis (E1). The linguliform brachiopods of the Shineton Shale Formation of Migneintian (late Tremadocian) age, also in Shropshire and described by Sutton *et al.* (1999, 2000) are also included (W2) and, from further south, the faunas in the Tortworth Inlier of Gloucestershire in the Micklewood and Breadstone Formations (Cressagian, W1).

However, slightly later latest Dapingian and early Darriwilian rocks in NW Wales to the NW of the Bala Fault, such as the Anglesey fauna of the Treiorworth Formation (W6) (late Floian) described by Bates (1968) and revised by Neuman & Bates (1978), carry more diverse brachiopods, many different from those in SW Wales. That is perhaps because they may not have been as close to SW Wales during Early Ordovician time as they are today, and were probably at a slightly lower palaeolatitude. Nevertheless, both the Anglesey and Shropshire faunas can both be identified as variants of Group 2 of the Mediterranean Province, although the Anglesey faunas are mostly of a slightly later age than the majority of faunas considered in this paper.

The contemporary higher-latitude trilobites were included within the calymenacean–dalmanitacean Province; however, its extent only partly overlapped the brachiopods of the Mediterranean Province during Early Ordovician time (Fortey & Cocks, 2003). It is also important to recognize that Avalonia was an integral part of the higher-latitude Mediterranean Province only during Early Ordovician time, since that microcontinent's independent drift across the closing Iapetus Ocean and behind the widening Rheic Ocean ensured that it progressively entered much lower latitudes during Darriwilian and later Ordovician times (Torsvik & Cocks, 2017). The Floian and Dapingian age brachiopods considered here are therefore almost the final representatives of the true Mediterranean Province in the Avalonian microcontinent. Since the Floian and Dapingian bivalves found in Carmarthenshire are the earliest known from Gondwana (Cope, 1996), this also appears to reflect the slightly lower latitude of South Wales during Early Ordovician time by comparison with much of the rest of the Mediterranean Province area.

Western Avalonia is the western limit of the large lingulides of the *Lingulobolus* Association. In particular, *Lingulobolus affinis* (Billings, 1872) occurs in substantial numbers in Bell Island, Newfoundland (Fig. 1, locality 8), where it forms a monotaxic community. However, that fauna has not been included in our statistical analysis since it cannot be discriminated from the similarly monotaxic *Lingulobolus* Association of NW Africa (Popov *et al.* 2019).

5. North Africa

Lower Ordovician rocks crop out in many areas of North Africa (Fig. 1, localities 5 and 6), where Torsvik & Cocks (2011, fig. 6), plotted many sites of the distinctive large lingulides of the Mediterranean Province on a 480 Ma palaeogeographical reconstruction. The Ordovician brachiopods of Morocco were

described by Havlíček (1971) and Mergl (1981), and some of the larger Group 1 lingulides from Algeria (KA) by Legrand (1971) and Popov *et al.* (2019); of Libya and Tunisia by Massa *et al.* (1977); and of Algeria and Morocco by Mergl (1983). Havlíček (1971) reviewed other North African areas and noted more Group 1 sites there. We have included brachiopods from the Upper Fezouata Formation (Arenig: Floian) of Morocco (M) from Videt *et al.* (2010), and a monotaxic *Lingulobolus* Association from the uppermost Kheneg el Aatène Formation of the Ougarta Range, Algeria (KA), in our analysis.

6. Middle East and Iran

Early Ordovician brachiopods are in general poorly known from southwestern Asia (the Middle East), but there are many and varied terranes in the region south and SW of the Altiid Fold Belt in Kazakhstan and adjacent countries. Some were integral sectors of Gondwana during Early Ordovician time, but most were independent peri-Gondwanan terranes (Popov & Cocks, 2017). However, because they spanned a wide range of palaeolatitudes, none of the brachiopod faunas can definitely be classified within the Mediterranean Province, and most were within the Intermediate Latitude Province to its then north. The latter include the Taurides of Turkey (then an integral sector of Gondwana), Karakorum and the various terranes within modern Iran (Fig. 1, locality 10) such as the Alborz and Lut terranes (Cocks & Torsvik, 2013). A relatively representative record of the Early Ordovician faunas currently exists only for the Alborz Terrane (Popov *et al.* 2008, 2009, 2013b; Ghobadi Pour *et al.* 2011; Kebria-ee Zadeh *et al.* 2015). While Mediterranean affinities prevail among the linguliform brachiopod associations, the rhynchonelliform brachiopod fauna became increasingly similar to the contemporaneous fauna of South China by the end of Early Ordovician time, as well as also including some endemic genera. Our analysis includes brachiopods from two levels in the Simeh–Kuh Formation – one in the middle Tremadocian Stage (*Paltodus deltifer deltifer* Zone, I1) and the other in the uppermost Tremadocian Stage (*Drepanoistodus* aff. *amoenus* Subzone, I2) – and three levels from the Qumes Formation – Gerd–Kuh Member (Floian, *Prioniodus elegans* Zone, I3), the Raziabad Member (uppermost Floian–lower Dapingian, I4) and a further member of the lower Dapingian Stage (*Baltoniodus navis* Zone, I5).

7. South and Central America

Early Ordovician brachiopods are known from several parts of the western and southern parts of South America (Fig. 1, locality 11), including Bolivia (Havlíček & Branisa, 1980) and Argentina (Benedetto, 2003), but the bulk of today's continent was then land. Nevertheless, when describing aspects of the Tremadocian brachiopods of the Central Andean Basin in NW Argentina, particularly the eoarthrid *Apheoarthina*, Muñoz & Benedetto (2016) noted that 64% of the genera in that fauna are shared with the Mediterranean area, particularly Bohemia, but the larger lingulates have not been recorded in South America.

From Argentina (not the Famatina Basin in the Precordillera, only Western Puna and the North-west Basin), Benedetto & Carrasco (2002), Benedetto (2009), Benedetto *et al.* (2009), Villas *et al.* (2009), Benedetto & Muñoz (2015, 2017) and Lavié & Benedetto (2020) recorded brachiopods included in our analysis. Within sample A1 are grouped the Las Vicuñas Formation (mainly

Table 3. Tremadocian – early Dapingian brachiopod genera of the Baltic Province (Baltoscandian Basin), South Urals (extension of the Mediterranean Province) and Alborz Terrane (mixed affinities to the faunas of Mediterranean Province and South China)

Locality and unit	Uralian margin of Baltica					Baltoscandian Basin, North Estonia and Ingria					Wyszczki Chalcedonite Formation, Poland	Alborz Terrane, Iran				
	Alimbet Formation	Kidryas Formation	Akbulaksai Formation	Koagash Formation	Khmelevka Formation	loa Member	Mäekula Member	Vasilkovo Member	Päite Member	Saka Member		Simeh- Kuh Formation	Simeh- Kuh Formation	Gerd Kuh Member	Raziabad Member	Qumes Formation
	SU1	SU2	SU3	SU4	SU5	EB1	EB2	EB3	EB4	EB5	P	I1	I2	I3	I4	I5
LINGULOIDEA																
<i>Dienecobolus</i>											+					
<i>Expellobolus</i>						+										
<i>Faveola</i>						+										
<i>Ferrobolus</i>				+												
<i>Hyperbolus</i>					+											
<i>Lamanskya</i>			+	+												
<i>Leptembolon</i>	+		+			+					+			+		
<i>Lingulella</i>						+										
<i>Palaeoglossa</i>		+														
<i>Paldiskia</i>						+										
<i>Paterula</i>									+	+						+
<i>Rowellella</i>										+	+					
<i>Thysanotos</i>			+			+									+	
<i>Wahwahlingula</i>												+	+			
ACROTHELLOIDEA																
<i>Orbithele</i>		+				+					+					
ACROTRETROIDEA																
<i>Akmolina</i>											+	+				+
<i>Acrotreta</i>			+		+		+	+	+							
<i>Aipyotreta</i>																+
<i>Ditreta</i>																+
<i>Dactylotreta</i>		+										+				
<i>Eoconulus</i>											+	+				
<i>Eurytreta</i>	+	+	+		+						+	+				
<i>Ghavidelia</i>													+			
<i>Mamatia</i>																
<i>Numericoma</i>										+						+
<i>Otariconulus</i>				+												
<i>Ottenbyella</i>														+		
<i>Pomeraniotreta</i>											+					
<i>Scaphelasma</i>										+						

(Continued)

Table 3. (Continued)

Locality and unit	Uralian margin of Baltica					Baltoscandian Basin, North Estonia and Ingria					Wyszczki Chalcedonite Formation, Poland	Alborz Terrane, Iran				
	Alimbet Formation	Kidryas Formation	Akbulaksai Formation	Koagash Formation	Khmelevka Formation	loa Member	Mäekula Member	Vasilkovo Member	Päite Member	Saka Member		Simeh- Kuh Formation	Simeh- Kuh Formation	Gerd Kuh Member	Raziabad Member	Qumes Formation
	SU1	SU2	SU3	SU4	SU5	EB1	EB2	EB3	EB4	EB5	P	I1	I2	I3	I4	I5
SIPHONOTRETOIDEA																
<i>Acanthambonia</i>											+					+
<i>Alichovia</i>											+					+
<i>Collarotretella</i>																
<i>Eosiphonotreta</i>						+	+	+						+		+
<i>Schizambon</i>						+										
<i>Siphonobolus</i>		+	+									+				
<i>Siphonotretella</i>				+							+					
PATERINOIDEA																
<i>Lacunites</i>			+					+								
PLECTAMBONITOIDEA																
<i>Leptastichidia</i>																+
<i>Leptella</i>									+	+						
<i>Plectella</i>							+	+	+							
POLYTOECHIOIDEA																
<i>Antigonambonites</i>								+	+	+						
<i>Korinevskia</i>					+											
<i>Martellia</i>														+	+	
<i>Raunites</i>										+						
<i>Tritoechia</i>												+				
CLITAMBONITOIDEA																
<i>Oslogonites</i>							+			+						
<i>Palaoneumania</i>								+	+	+						
ORTHOIDEA																
<i>Alimbella</i>	+		+													
<i>Altorthis</i>	+		+				+	+								
<i>Apheorthina</i>							+									
<i>Archaeorthis</i>	+	+	+													
<i>Astraborthis</i>											+					
<i>Glossorthis</i>											+					
<i>Leoniorthis</i>								+	+	+						
<i>Medessia</i>	+	+														

(Continued)

Table 3. (Continued)

Notorthis				+																
Ocarthis							+													
Orthidium												+								
Panderina																				
Productarthis																				
PLECTORTHIOIDEA																				
Ranorthis																				
DALMANELLOIDEA																				
Angusticardinia																				
Paurorthis																				
SYNTROPHIOIDEA																				
Camerella																				
Diaphelasma																				
Eoporambonites																				
Iliostrophia																				
Porambonites																				
Tetralobula																				

Tremadocian *Cordylodus angulatus* Zone), the lower Tremadocian Guayoc Chico Group, Cardonal Formation and the Devendeus Formation. In sample A2 (late Tremadocian, *Paltodus deltifer* and *Paroistodus proteus* zones) we have grouped the Santa Rosita Formation, the Saladillo Formation, the Coquena Formation, Upper Member and an unnamed sandstone in Salta Province. Within sample A3 are grouped the Floresta Formation and the Upper Suri Formation (late Floian, *Oepikodus evae* Zone), while the fauna from the Molles Formation (late Floian – early Dapingian?) is listed separately (A4).

From southern Mexico, Streng *et al.* (2011) described the late Cambrian and Tremadocian inarticulated brachiopods from what was then the Oaxaquia Microcontinent (Fig. 1, locality 8) and recorded seven genera from the upper half of the Teñu Formation, the acrotretoids *Eurytreta?*, *Ottenbyella?* and *Semitreta*, the endemic siphonotretoid *Oaxaquitreta*, and three unidentified linguloids, an obolid and *Lingulella?*. While not a clear-cut Mediterranean Province fauna, that assemblage can be interpreted as representing a cline between it and the Intermediate Latitude Province, as might be expected from Oaxaquia's estimated position at about 35° S; however, that fauna has not been included in our statistical analysis.

8. Baltica

During the Furongian and Tremadocian ages, the South Uralian margin of Baltica continent was located in high southern latitudes (Fig. 1, localities 12–14), probably at > 60° S. It was facing the Mediterranean margin of Gondwana and was separated by a narrow ocean from the Gondwana margin (Torsvik & Cocks, 2017). The Lower Ordovician linguliform brachiopod fauna of the South Urals was monographed by Popov & Holmer (1994), and the billingsellides were revised by Popov *et al.* (2001). Published data on the rhynchonelliform brachiopods (Andreeva, 1960; Nasedkina, 1977) are very outdated, but they are supplemented by a further collection originally made by VV Korinevskii and currently under revision in the National Museum of Wales; the genera analysed here have therefore all been newly reassessed by LEP. The Early Ordovician linguliform brachiopods of the South Urals are very similar to the contemporaneous faunas of Bohemia and Alborz (Popov *et al.* 2013a). The moderately rich Floian rhynchonelliform brachiopod fauna from the South Urals includes a considerable proportion of endemic genera, yet the presence of *Protambonites* is a clear signature of the Mediterranean Province, as well as the occurrence of the trilobite *Asaphellus*. The linguliform brachiopods also show distinct similarity to those in Gondwana. Faunas included in our analysis include those from the Alimbet Formation (Tremadocian, SU1), the Kidryas Formation (Tremadocian, *Paltodus deltifer* Zone equivalent, SU2), the Akbulaksai Formation (lower Floian, SU3), the Koagash Formation (upper Tremadocian, SU4) and the Khmelevka Formation (Tremadocian, SU5).

From the area on the eastern side of the Baltic Sea itself (Fig. 1, locality 13) we have analysed more newly reidentified brachiopods from the Leetse Formation: the Ioa Member in North Estonia (Floian, *Paroistodus proteus* Zone, EB1); the Mäekula Member in Tallinn, Estonia and the Popovka Stream near Pavlovsk, Ingria, Russia (Floian: *Prioniodus elegans* Zone, EB2); the Vasilkovo Member from the Popovka Stream near Pavlovsk and the Lava River, Ingria (Floian, *Oepikodus evae* Zone, EB3); the Päite Member (Floian, *Oepikodus evae* Zone) of the Volkhov Formation in the Lava and Syas rivers, Ingria (EB4); and the Saka Member (Dapingian, *Baltoniodus triangularis* – *B. navis* Zones), also of the Volkhov Formation (EB5).

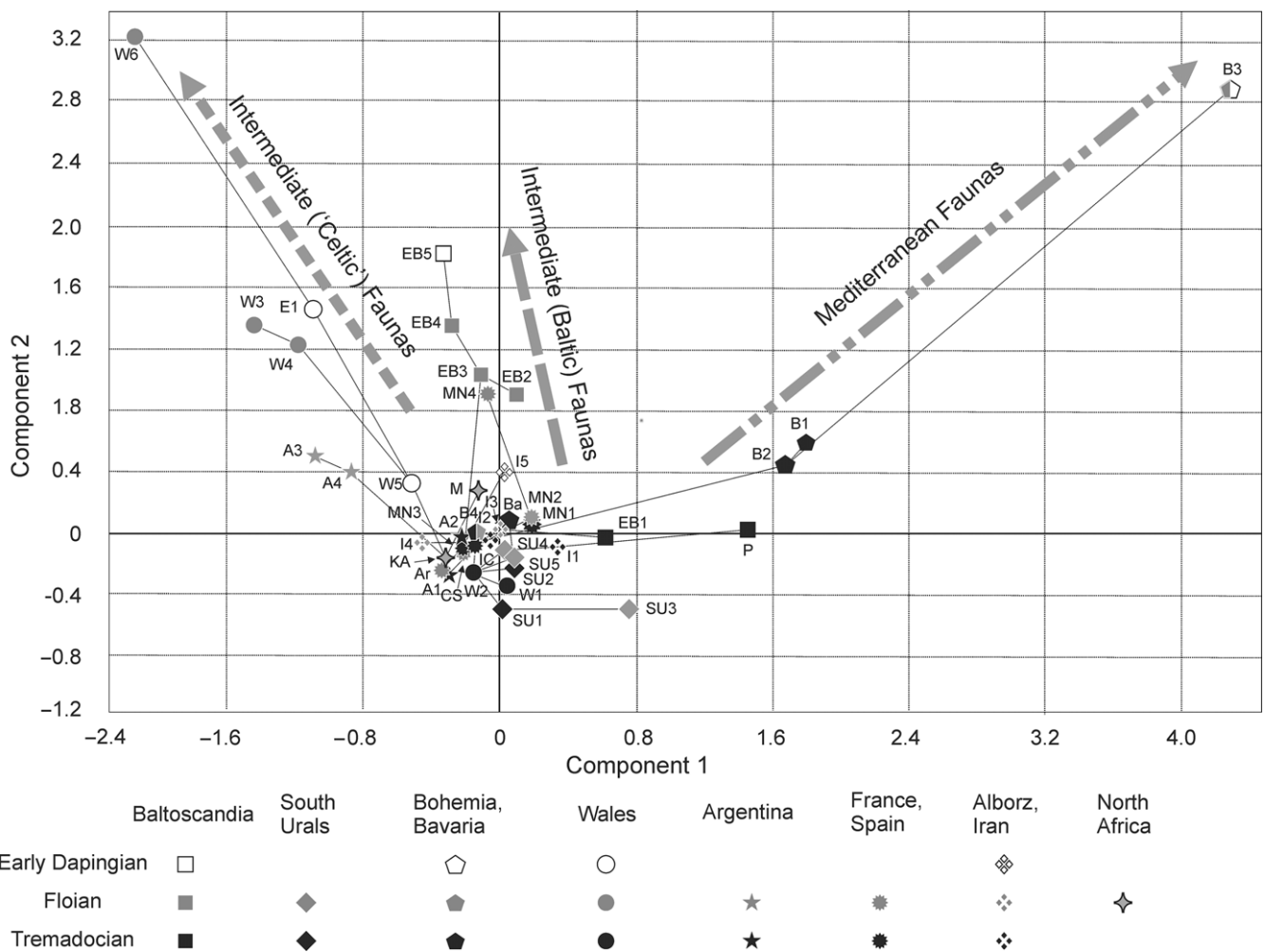


Fig. 2. Two-dimensional PCA plots on first and second eigenvectors of 163 brachiopod genera from 37 localities of Tremadocian–Dapingian ages from the Mediterranean Province core including Bohemia, Bavaria, Armorican Terrane Assemblage and North Africa, plus other contemporary faunas including Central Andean Basin, Avalonia, Alborz (Iran) and the Baltica continent. B1, Třenice Formation (Tremadocian), Bohemia; B2, Milina Formation (upper Tremadocian), Bohemia; B3, Klabava Formation (Floian), Bohemia; B4, Železná hora (late Tremadocian – early Floian), east Bohemia; B2, Milina Formation (late Tremadocian), Bavaria; W1, Tortworth Inlier, Gloucestershire (Cressagian); W2, Shineton Shale (Migneintian), Shropshire; W3, Ogof Hên Formation (Floian), Wales; W4, Blaencediw Formation (Floian), Wales; W5, Pontyfenni Formation (Dapingian), Wales; W6, Treiorworth Formation (Floian), Anglesey, Wales; Ar, Armorican Quartzite (Floian), Normandy, France, including Budleigh Salterton, England; MN1–4, Montagne Noire, France; MN1 Foulon Formation (Floian–Dapingian); MN2, La Maurerie Formation (Floian); MN3, Cluse de l'Orb Formation (Floian); MN4, Landeyran Formation (Floian); CS, Cabos Series (Tremadocian), Iberian Chains, Spain; M, Upper Fezouata Formation (Floian), Morocco; A1–A3, Tremadocian, Famatina Basin, Argentina; A3, Suri Formation (Floian), Argentina; I1–I3, Alborz, Iran; I1, Simeh-Kuh Formation (Tremadocian); I2, Simeh-Kuh Formation (late Tremadocian); I3, Qumes Formation, Gerd-Kuh Member (Tremadocian); EB2 and EB3, Leetse Formation (Floian), Estonia and Ingria; EB3, Leetse Formation, Vasilkovo Member (Floian), Ingria, Russia; EB4, Volkhov Formation, Päite Member (Floian), Ingria, Russia; EB5, Volkhov Formation, Saka Member (Dapingian), Ingria, Russia; P, Miedzygórz Beds (middle Tremadocian), Holy Cross Mountains, Poland; SU1–SU5, South Urals; SU1, Alimbet Formation (late Tremadocian); SU2, Kidryas Formation (middle Tremadocian); SU3–4, Akbulaksai Formation (early Floian); SU5, Khmelevka Formation (Tremadocian).

In the Holy Cross Mountains of Poland (Fig. 1, locality 14), the largely inarticulated brachiopods from the underlying Miedzygórz Beds (Tremadocian, P) were described by Biernat (1973) and Holmer & Biernat (2002). Above them lie the Lower Bukówka Beds whose brachiopods were reviewed in Cocks (2002) and included *Plectella*, *Lycophoria*, *Paurorthis*, *Antigonambonites* and *Syntrophina*? They are probably of late Floian age, but may be of earliest Dapingian; in either case they represent a well known assemblage that is very characteristic of the Baltic Province since it was entirely confined to that continent during Early Ordovician time.

9. Palaeogeography and analysis

The new biogeographical analysis of the Early Ordovician brachiopod faunas is based on the extensive database assembled by the

authors, which includes 167 rhynchonelliform and linguliform genera representing 42 individual faunas varying in age from middle Tremadocian to early Dapingian. The dataset was subjected to cluster analysis (Raup–Crick Similarity Index) and a principal components analysis (PCA) using the PAST (palaeontological statistics) programme (Hammer & Harper, 2006, Hammer *et al.* 2014).

The data sources used in the analysis are heterogenous. Most of the individual faunas are simply lists of taxa that occur in a single lithostratigraphical unit. However, in several cases they represent time slices that include several lithostratigraphical units; for example, the inarticulated brachiopods from British regional stages revised by Sutton *et al.* (1999, 2000) and the Tremadocian faunas of Argentina. Faunas derived from a single lithostratigraphical unit may belong to a single, sometimes monotoxic, community (e.g. the

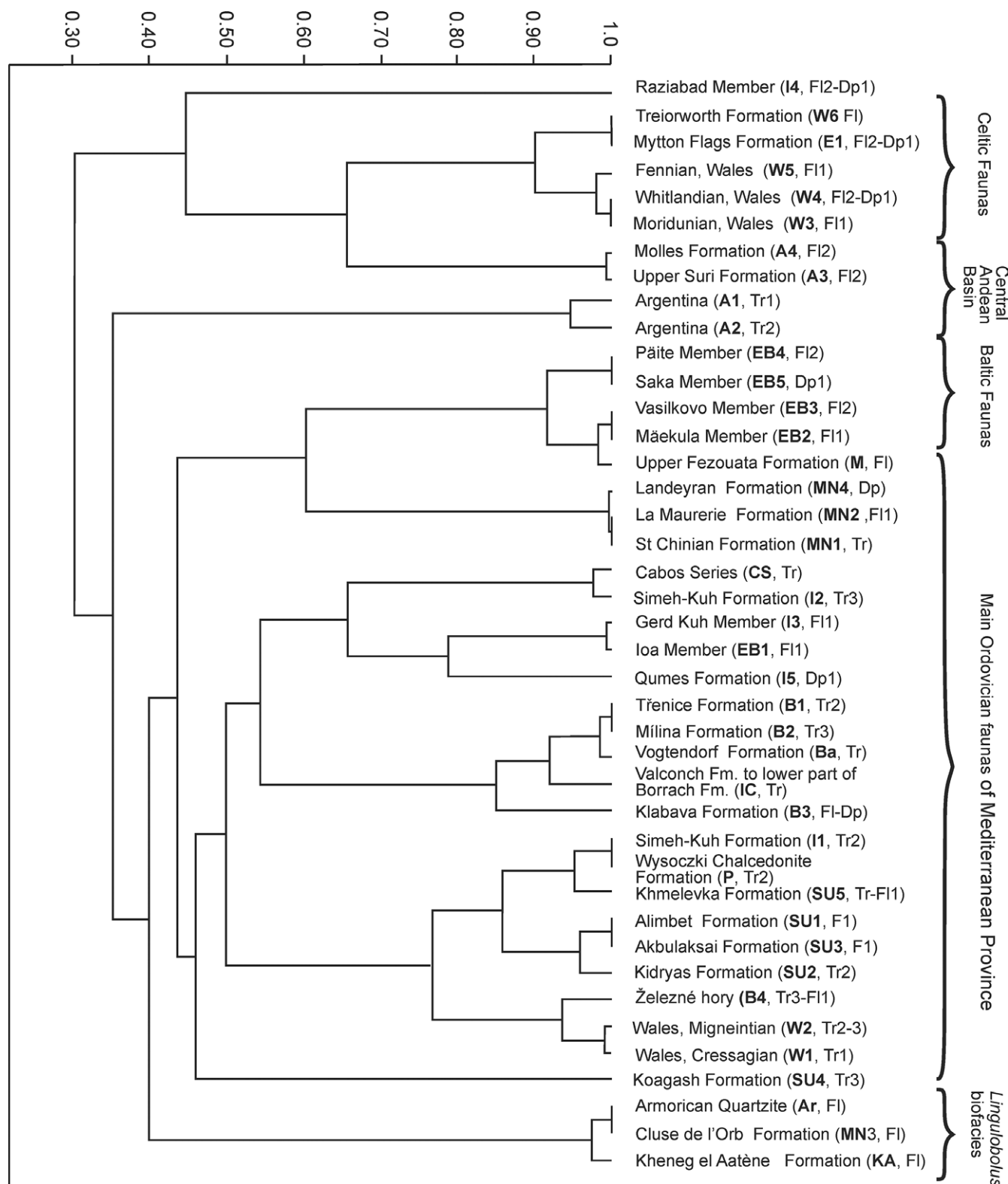


Fig. 3. Cluster analysis (using Raup–Crick Similarity Index) of 163 brachiopod genera from 37 localities of Tremadocian–Dapingian ages from the Mediterranean Province core including Bohemia, Bavaria the Armorican terrane cluster, and North Africa, as well as contemporaneous faunas from the Central Andean Basin, Avalonia, Alborz (Iran), and the Baltica continent.

Cabos Series of the Iberian Chains) or a number of different communities (e.g. the Třenice, Milina and Klabava formations of Bohemia). However, our data still permits us to trace the biogeographical differentiation of the brachiopod faunas within the

Mediterranean Province area, the possible centres of origin and initial dispersion of certain key taxa and entire communities, and the faunal divergence caused by the progressive drifting apart of the Baltica and Avalonia continents.

The end of the Cambrian Period was a time of substantial decline of linguliform brachiopod faunas (Bassett *et al.* 1999) especially evident in the acrotretides, with only six genera crossing the Cambrian–Ordovician boundary. A significant turnover also occurred in the lingulide communities nearshore. The distinctive obolid fauna of the Baltoscandian basin disappeared without descendants near the beginning of the Tremadocian Age (Popov *et al.* 1989). The observed patterns of the linguliform biogeographical distribution across the Mediterranean Province in the Tremadocian were therefore due to post-extinction recovery and dispersal. The biofacies differentiation of the Tremadocian–Floian linguliform brachiopod faunas is best documented in Bohemia, as summarized by Mergl (2002).

The biogeography of the Tremadocian rhynchonelliform brachiopods is poorly constrained because of the relatively small number of localities and low-diversity individual faunas known from across the world; however, broadly low-latitude and high-latitude provinces can be recognized (Harper *et al.* 2013). Further analysis of the mixed linguliform and rhynchonelliform brachiopod assemblages in this paper has also revealed some links helpful for a better understanding of the changing biogeographical patterns in brachiopod dispersal across the southern latitudes during Early Ordovician time.

PCA shows that the Early Ordovician faunas of Western Mediterranean Gondwana, North Africa, Argentina, the Alborz terrane of Iran and the Uralian margin of Baltica formed a compact cluster together with the Tremadocian faunas of Avalonia and Tremadocian – early Floian fauna of the East Baltic (Fig. 2). Remarkably, they completely lack any rhynchonelliform component, which suggests that such clustering is defined in significant part by the geographical distribution of the linguliform taxa. The cluster is characterized by low to moderate negative scores along the second direction of variations, and low negative to low positive scores (–0.8 to 0.8) along the first direction of variations. The only visible differentiation can be seen in the distribution of the Argentinian and Uralian faunas: the latter are characterized by exclusively positive scores along the first direction of variations against the negative scores characteristic of the Argentinian faunas.

Surprisingly, almost all the Early Ordovician brachiopod faunas of Bohemia are placed outside the main cluster of the faunas here assigned to the Mediterranean Province (Fig. 2). They are characterized by positive scores along the second direction of variation and higher positive scores along the first direction of variations, both increasing in time from the Tremadocian to the Dapingian ages. The Early Ordovician Bohemian brachiopod faunas are characterized by the high endemism of rhynchonelliform brachiopods represented by the monotaxic family Poramborthisidae (Mergl, 2011) and the high proportion of endemic orthide genera, for example, *Ferrax*, *Nocturniella* and *Robertorthis*. In contrast, the eorthid *Jivinella* and endopunctate *Nereidella* represent some contact with South China, although they are missing from other Mediterranean faunas. The Early Ordovician linguliform means of Bohemia are outstandingly rich in the generic composition of the assemblages, with many genera in high to temperate southern latitudes unknown from other contemporary faunas.

The Floian to early Dapingian brachiopod faunas of Avalonia are also placed outside the main cluster of the Mediterranean faunas, and show strongly negative scores along the first direction of variations and positive scores along the second direction of variations. Similar tendencies can be seen in the distribution of the Moridunian and Whitlandian linguliform brachiopod faunas

(Fig. 2), which is probably a sign of steadily increasing biogeographical divergence.

In the cluster analysis (Raup–Crick Similarity Index), the Moridunian–Floian faunas of Avalonia appear quite distant from other analysed faunas of the Mediterranean Province plus Baltic faunas, forming a separate first-order cluster together with the Floian Argentinian faunas of the Suri and Molles formations (Fig. 3). The Avalonian fauna includes a large proportion of endemic genera (*Astraborthis*, *Rhynchorthis*, *Rectotrophia* and *Treioria*) or genera that are otherwise known only from the Floian Stage of the Central Andean Basin (*Ffynnonia*, *Monobolina*, *Monorthis*, *Skenidioides*, *Protoskenidioides*, *Rugostrophia* and *Productorthis*), although some of them make later appearances outside those regions. The plectambonitoidean taffiids *Aporthophyla*, *Taffia* and *Inversella* (*Reinversella*) make their earliest appearances in Avalonia, which can therefore be considered as the centre of their origin and initial dispersal.

Similarly, the Floian brachiopod fauna of the Central Andean Basin (A3, A4) also contains a significant proportion of local endemics, including *Famatinobolus*, *Chilcatreta*, *Incorthis*, *Mollesella*, *Suriorthis*, *Punastrophia* and the earliest occurrence of the taffiid *Ahtiella*, and is characterized by the relative abundance of the earliest skenidiids (*Crossiskenidium*, *Skenidioides* and *Protoskenidioides*). Not surprisingly, in the cluster analysis it shows a significant degree of separation from the other Mediterranean faunas and clusters together with British faunas (Fig. 3).

The Tremadocian faunas of the Central Andean Basin (A1, A2) grouped in a separate second-order cluster (Fig. 3). They are characterized by the relative abundance of the early plectrothoid genera (*Euorthisina*, *Gondwanorthis*, *Incorthis*, *Lampazarorthis*, *Lesserorthis*, *Kvania*, *Notorthisina* and *Tarfaya*) assigned by Benedetto & Muñoz (2015) to the reincarnated family Nanorthidae. They were mostly short-lived local endemics forming low-diversity associations, but some of them show wider geographical distributions. *Gondwanorthis* is also known from the middle Tremadocian Stage of Iran, *Incorthis* from the Tremadocian Stage of Bolivia and Morocco, and *Kvania* from the Mílina Formation of Bohemia (Havlíček *et al.* 1994) and Bavaria (Sdzuy *et al.* 2001). The Tremadocian rhynchonelliform brachiopod faunas of the Central Andean Basin include the earliest documented representatives of the families Euorthisinidae (*Euorthisina* and *Notorthisina*), Tarfayidae (*Tarfaya*) and Anomalorthisidae (*Astraborthis*). By Floian time, the Euorthisinidae had dispersed to Avalonia, Bohemia, North Africa and South China (Gutiérrez-Marco & Villas, 2007). *Notorthisina* is probably phylogenetically closely related to *Lipanorthis* (Benedetto & Muñoz, 2017), which is the earliest yet known endopunctate orthide. The Anomalorthisidae also proliferated in Floian time when they are known from Avalonia and the Uralian margin of Baltica (*Alimbella* and *Medesia*), and by the Darriwilian Age had dispersed to Laurentia (*Anomalorthis*). *Tarfaya* spread widely during middle–late Tremadocian time across Gondwana, being reported from North Africa, Alborz in Iran and Tasmania as a part of monotaxic or oligotaxic brachiopod communities; it often forms characteristic shell beds nearshore. According to the phylogenetic analysis of Benedetto & Muñoz (2017), *Tarfaya* is most probably the ancestral taxon of the endopunctate family Heterorthisidae, which later played a significant role in the Middle–Late Ordovician brachiopod faunas of the Mediterranean Province. In Tremadocian time, the Central Andean Basin was therefore an important brachiopod biodiversity hotspot and a cradle for several lineages that dispersed during late Tremadocian – Floian time

across the Mediterranean Province and beyond, including the endopunctate orthides, which played a very important role within the Late Ordovician faunas of the Mediterranean Province.

The linguliform brachiopods of the Central Andean Basin are incompletely known, especially their acrotretide and siphonotretide components, yet they include typical Mediterranean genera such as *Leptembolon* and *Libecoviella*, while *Monobolina* there is otherwise known only from East Avalonia (Benedetto & Muñoz, 2015; Lavié & Benedetto, 2020).

The core of the Early Ordovician Mediterranean Province is formed by the Tremadocian faunas of Avalonia and Early Ordovician faunas of Bohemia, Bavaria, Montagne Noire, Spain and the South Urals (Fig. 3). It also includes the Tremadocian faunas of Alborz (Iran) and the middle Tremadocian – early Floian linguliform brachiopod faunas of Baltica. In the cluster analysis (Rau–Crick Similarity Index) it appears as a separate subclade within the third-order clade together with the faunas of the emerging Baltica Province. That is not surprising since there are no documented rhynchonelliform brachiopod faunas across Baltica through late Cambrian (Furongian) time, except those from Novaya Zemlya (Holmer *et al.* 2020) and the pioneering moderately rich Floian rhynchonelliform associations from middle–late Floian time of Baltoscandia that emerged suddenly due to immigration, most probably from the temperate-latitude sector of Gondwana (Stuesson *et al.* 2005). Indeed, the brachiopod assemblages from the Mäekula and Vasilkovo members (*Prioniodus elegans* to *Oepikodus evae* zones) of Estonia and Ingria contain, in addition to the neoendemics *Eoporambonites*, *Leoniorthis*, *Lycophoria*, *Panderina*, *Plectella* and *Porambonites*, a sizeable fraction of genera otherwise characteristic of the Mediterranean Province, for example, *Angusticardinia*, *Apheoorthina*, *Ocothis*, *Paurorthis*, *Prantlina* and *Ranorthis* (Havliček, 1971, 1977; Mélou, 1982). It is rather surprising that the brachiopod assemblage from the Upper Fezouata Formation (Floian) of Morocco appears to be closely linked to the earliest Baltoscandian brachiopod associations in the cluster analysis (Fig. 3), but that may simply be a coincidence.

In our analysis, Tremadocian–Floian faunas from the Montagne Noire (MN1, 2, 4) appear quite distant from the other faunas of the Mediterranean Province. Instead, they more closely cluster with the early Baltic faunas (Fig. 3). That affinity is mainly defined by the co-occurrence of linguliforms such as *Acrotreta*, *Rafanoglossa*, *Spondyglotella* and *Westonia*, but also by the rhynchonelliform genera *Ocothis*, *Prantlina* and *Ranorthis*. The latter three were also characteristic of the Floian of Baltoscandia (Rubel, 1964). The middle Floian rhynchonelliform brachiopod immigration event in Baltoscandia occurred synchronously with proliferation of the bryozoans, ostracods and agglutinated foraminifers as a part of the early dispersal of the benthic communities with the characteristic features of the Palaeozoic Evolutionary Fauna (Bassett *et al.* 2002). That immigration was preceded by the almost complete extinction of Furongian – early Tremadocian obolid and siphonotretide local lineages (Ghobadi Pour *et al.* 2017) and was followed by the invasion of the *Thysanotos–Leptembolon* linguliform brachiopod Association, which had originally evolved in the temperate latitudes of Gondwana (Bednarczyk, 1988, 1999; Popov & Holmer, 1994; Mergl, 1997, 2002). Dispersal of the latter fauna during late Tremadocian – early Floian time towards the Baltoscandian basin was therefore the time of maximum expansion of the Mediterranean Province.

The individual brachiopod faunas grouped within the Early Ordovician faunas of the Mediterranean Province core represent

mainly low- to medium-richness assemblages of linguliformean and rhynchonelliform brachiopods, often with little sign of biofacies differentiation. Linguliform brachiopods prevail within the Tremadocian faunas, yet rhynchonelliforms constitute a sizeable fraction within the faunas of Bohemia and Alborz, and the significance of rhynchonelliforms steadily increased during Floian time. The best studied Early Ordovician Mediterranean faunas are from Bohemia, where Mergl (2002) was able to recognize a number of depth-related brachiopod communities based on 82 individual localities. Some of them are important in the definition of the Mediterranean Province, and others give some clues about the origins of the individual faunas within the Province. Probably the most significant is the *Leptembolon* Community, which can be considered to be a local variation of the *Thysanotos–Leptembolon* Association. The latter was also widespread across Baltica, including the Klooga and Joa members (upper Tremadocian – lower Floian, *Drepanoistodus proteus* – *Prioniodus elegans* conodont zones) of North Estonia, the Zbilutka Beds (middle Tremadocian, *Paltodus deltififer* conodont Zone) of the Holy Cross Mountains in Poland (Bednarczyk, 1988), and the South Urals in the upper Tremadocian – lower Floian Alimbet and Akbulaksai formations (Popov & Holmer, 1994). In Alborz, Iran, the occurrence of the *Thysanotos–Leptembolon* Association is diachronous but is nevertheless confined entirely to the lower Floian *Prioniodus elegans* Zone (Popov *et al.* 2008). According to Mergl (2002), the Bohemian *Leptembolon* Community was characteristic of the lower shoreface to upper offshore transition; however, locally *Thysanotos* overlaps with the rhynchonelliform *Protambonites*, which is the dominant taxon in the oligotaxic to almost monotaxic rhynchonelliform communities nearshore in the South Urals and Alborz (Popov *et al.* 2001, 2009) and forms shell beds in the Cabos Series of the Cantabrian Mountains, Spain (Villas, 1995). The Bohemian *Hyperobolus* Community was confined to the mobile sands nearshore (Mergl, 2002), and in life strategies the characteristic taxa strongly resemble the Furongian nearshore obolid communities of the Baltoscandian basin (Popov *et al.* 1989). *Hyperobolus* also occurs in the South Urals in the shell beds formed by the polytoechioid *Korinevskia* in the Tremadocian Akbulaksai Formation (Popov *et al.* 2001). Those oligotaxic to monotaxic polytoechioid brachiopod associations, which produced characteristic shell beds nearshore at the Uralian margin of Baltica and temperate latitude Gondwana, seem to be related to the late Cambrian (Furongian) billingsellide associations (Bassett *et al.* 2002). The earliest polytoechioids are from the Furongian Stage of Alborz (Iran) and South China (Popov *et al.* 2013a), which were the likely regions for the origin and subsequent dispersal of the group.

The rhynchonelliform component of the Early Ordovician Bohemian fauna is represented predominantly by the orthides. Some of them were short-lived local endemics (*Ferrax* and *Robertorthis*); others (*Apheoorthina*, *Prantlina* and *Ranorthis*) subsequently migrated towards Baltoscandia. *Nocturnellia* from the Klabava Formation is the earliest genus of the Enteletoidea, another group of endopunctate orthides that achieved much eminence within the higher-latitude faunas during Late Ordovician time. The short-lived monotaxic family Poramborthisidae was relatively widespread in the Tremadocian Age, being documented from Bohemia (Havliček, 1977), Bavaria (Sdzuy, 1955; Sdzuy *et al.* 2001) and Spain (Havliček & Josopait, 1972), but it is unknown from Armorica, Avalonia, North Africa and South America.

The Bohemian faunas group closely together with other faunas from Bavaria (Ba) and Spain (CA), which are characterized by the

occurrence of *Porambortis* that has biogeographical significance (Harper *et al.* 2013), and more distantly with faunas in Iran (I2, I3, I5) and the late Tremadocian – early Floian faunas of the East Baltic (Ba1), characterized by the proliferation of the *Thysanotos–Leptembolon* Association. The later appearance of that association in the Baltoscandia and Alborz, Iran may indicate that Bohemia was a primary centre of dispersal of this linguliform fauna.

The Tremadocian (Cressagian–Migneintian) faunas of Avalonia (W1, W2) group with the Tremadocian–Floian faunas of the South Urals (SU1–3), mainly because of the co-occurrences of *Acrotreta*, *Broeggeria*, *Eurytreta*, *Semitreta* and *Orbithele*. Three of those genera (*Broeggeria*, *Eurytreta* and *Orbithele*) are common, but not entirely confined, to the cosmopolitan *Broeggeria* Association, since that association lived in dysaerobic environments with black mud accumulations that were widely dispersed (Bassett *et al.* 1999). The observed affinity therefore reflects the similar biofacies characteristic of marginal environments, rather than any indication of close biogeographical or provincial affinities.

Another example of marginal biofacies with distinctive taxonomic compositions that overweigh biogeographical signatures is the monotaxic to oligotaxic lingulide communities of BA1, which can be assigned to the *Lingulobolus* Association. They inhabited mobile nearshore sands and muds and often occur together with the *Cruziana* and *Skolithos* ichnofacies (Emig & Gutiérrez-Marco, 1997; Coke & Gutiérrez-Marco, 2001). The lingulide shells characteristic of the *Lingulobolus* biofacies form extensive shell beds that are chiefly within quartzites laid down under rather shallow water, as exemplified by the Grès Armoricaïn of northwestern France itself. McDougall *et al.* (1987) plausibly concluded that the Armorican Quartzite of the Central Iberia Zone of North Portugal was deposited in a variety of disconnected basins adjacent to various local land masses, and the quartzite is usually unconformable on Cambrian and earlier rocks, many of which had been disrupted by the late Precambrian and early Cambrian Cadomian Orogeny. We agree with that conclusion, which is in marked contrast with the enormous extent of an Armorican Quartzite sheet continuous over much of southern Europe and North Africa that had previously been wrongly postulated by some authors. That palaeogeographical condition favours the significant influx of siliciclastic sediments and seasonal freshwater runoff into the shallow basins, which created a favourable habitat for the strikingly distinctive large linguliform brachiopod assemblage.

All the Armorican Quartzites were previously assigned to be of ‘Arenig’ age, but are now considered as confined to middle and upper Floian time based on chitinozoan biozonation (Videt *et al.* 2010). Figure 1 shows the distribution of the other chief sites that have yielded Mediterranean Province brachiopods in earliest Ordovician time (late Tremadocian, Floian and early Dapingian), as well as some other contemporary brachiopod sites (not discussed in detail in the present paper apart from Baltica) that have yielded brachiopods attributable to other provinces in lower latitudes to the north of the Mediterranean Province; these are briefly reviewed in the next section.

In North Africa and West Avalonia the *Lingulobolus* lingulide community was often monotaxic (Popov *et al.* 2019); in southwestern Europe (France and Spain) and Cornwall, it also included *Ectenoglossa*, *Lingulepis*, *Rafanoglossa*, *Tomasina* and possibly *Lingulella*. The geographical area occupied by those lingulides was confined to subpolar latitudes of > 65° S. As pointed out by Emig & Gutiérrez-Marco (1997), the lingulid shell beds within

the area occupied by the *Lingulobolus* biofacies was often deposited by catastrophic events, as well as significant freshwater influx into the environment. Because of the high latitudinal position of the shores inhabited by these lingulides, the major source of that freshwater influx can probably be attributed to seasonal ice and snow melting (Popov *et al.* 2013a). The *Lingulobolus* Association includes a significant proportion of burrowing lingulides, which are among the earliest examples of the ‘*Lingula*’-type associations of Ziegler *et al.* (1968) that proliferated later through the Palaeozoic Era and have continued until the present day.

10. Intermediate latitude and equatorial provinces

Between the two lowest-latitude Equatorial provinces and the Mediterranean Province there were a variety of brachiopod faunas, grouped here as the Intermediate Latitude Province. The most distinctive Intermediate Latitude assemblage is that which surrounded the substantial continent of Baltica, which included a host of endemic taxa including the orthide *Lycophoria*, the only genus in its family, and most of the genera within the superfamilies Clitambonitoidea and Gonambonitoidea (see also Section 8 above). In contrast, the quite different Asian Intermediate Latitude faunas included a community dominated by the large syntrophoid *Yangtzeella*, which was originally described from South China, but is now also known from the Taurides of Turkey (then an integral sector of Gondwana), Karakorum and Iran (Cocks & Torsvik, 2013), as well as some more cosmopolitan genera. In addition, to the west of Gondwana and largely in South America today, there were less distinctive assemblages that were largely dominated by more cosmopolitan genera. Also included in the Intermediate Latitude Province is what some authors, summarized by Harper *et al.* (2013), termed the Celtic Province, although that term has been interpreted in different ways by a variety of authors and it has not been conclusively identified from any rocks older than the late Dapingian in age.

The shallow-water benthos in the Equatorial latitudes were divided into two provinces: the Laurentian Province, which was principally in North America, including the diverse brachiopod genera that have not been comprehensively revised since the classic paper by Ulrich & Cooper (1938); and the Cathay–Tasman Province, which included that substantial sector of Gondwana that straddled the Equator, including Sibumasu (which remained an integral part of Gondwana throughout early Palaeozoic time), Australia, and the independent North and South China continents (Torsvik & Cocks, 2017).

11. Conclusions

During Early Ordovician time, the varied brachiopod benthic communities of the Mediterranean Province were extensively developed in the latitudes then > *c.* 55° S, largely at the margins of the large Gondwana continent but also in neighbouring terranes. The individual Early Ordovician Mediterranean faunas from temperate and high latitudes represent loose, commonly low-diversity associations of rhynchonelliform and linguliform brachiopods that were variable in taxonomic composition. They were often a mixture of cosmopolitan genera (mostly linguliforms) and some local endemics (both linguliforms and rhynchonelliforms). Some of them were probably the last occurrences of Cambrian (Furongian) lineages; others were neoendemics either representing local, short-lived genera, or taxa at the base of the Ordovician lineages, most importantly in the Andean Basin and Avalonia. The

complex palaeogeographical patterns in the distribution of linguliform brachiopods across the high to temperate latitudes of Gondwana through Early Ordovician time can be explained by the gradual replacement within benthic communities of new taxa of the Cambrian Evolutionary Fauna (dominated by trilobites and linguliform brachiopods) within the early communities of the Palaeozoic Evolutionary Fauna, in which the rhynchonelliform brachiopods were major components, and with increasing numbers of locally abundant bryozoans, bivalves, ostracods and pelmatozoan echinoderms. The rhynchonelliform communities of the latter type first appeared in the Tremadocian Stage of the Andean basin (Benedetto *et al.* 2009; Benedetto & Muñoz, 2017) and the Alborz region of Iran. The latter can be considered as on the periphery of the major Early Ordovician biodiversity hotspot centred within the South China continent (Harper *et al.* 2013; Zhan & Jin, 2014). These rhynchonelliform-dominant communities were originally characteristic of the lithofacies of the upper offshore and onshore-offshore transition (BA3-4), which during late Tremadocian and early Floian time dispersed towards the shore (e.g. the *Tarfaya* Community in Argentina, Morocco and Alborz) and further down into the deeper shelves and basins. The *Protambonites* community inherited the position of the Furongian nearshore billingsellide communities, but it coexisted for some time with the *Tarfaya* Community (Popov *et al.* 2009; Benedetto & Muñoz, 2017), which had similar life strategies. By the Darriwilian Age, the latter had evolved in North Africa into the monotaxic, heterorthid *Tissintia* Community (Popov *et al.* 2019), which formed a central feature of the Middle Ordovician Mediterranean Province, while polytochiid communities nearshore had already disappeared by Dapingian time.

The *Thysanotos–Leptembolon* Association, distinctive in its large epibenthic lingulides, made its earliest appearance in Bohemia and then dispersed within temperate latitudes (mainly > 65°) on both sides of the narrow west branch of the Ran Ocean. Its proliferation in the environments of BA2 and BA3 can be considered as the ‘last stand’ of the Cambrian Evolutionary Fauna. In South Urals, Bohemia and Alborz they coexisted for some time, but were then gradually replaced by the rhynchonelliform brachiopod communities at the end of the Floian Age. In Baltica, the *Thysanotos–Leptembolon* Association was sharply replaced by a newly immigrant fauna of rhynchonelliform brachiopods, bryozoans, ostracodes and echinoderms in middle Floian time. A similar sharp replacement of the linguliform brachiopod associations by the benthic communities with characteristic features of the Palaeozoic Evolutionary Fauna occurred during early Floian time in East Avalonia (Cocks & Popov, 2019), with the rich mollusc-brachiopod association from the Ogof Hên Formation of SW Wales as a good example (Cope, 1996).

Unlike the *Thysanotos–Leptembolon* Association, the *Lingulobolus* Association seems best considered as the earliest example of the ‘*Lingula*’-type associations that subsequently evolved within the community structure characteristic of the Palaeozoic Evolutionary Fauna. The Tremadocian–Floian high-latitude rhynchonelliform brachiopod faunas are relatively scarce, of low diversity and still not well known. In the Armorican terrane cluster they include only *Poramborthis* and *Protambonites* (Havlíček & Josopait, 1972; Villas, 1995), while in the Tremadocian Stage of Morocco (the Lower Fezouata Formation) Havlíček (1971) listed only *Saccogonum*, *Ranorthis* and “*Plectorthis*”, although the latter generic identification is questionable. All those genera are also present in the Floian Upper Fezouata

Formation, where they are accompanied by *Angusticardinia*, *Paurorthis* and *Tarfaya*, all taxa that occupied a more offshore position, meaning that their areas did not overlap with the lingulide communities.

Although the large inarticulated lingulides were confined to Early Ordovician time, the more diverse assemblages can be recognized as continuing aspects of the Mediterranean Province up to near the end of the Ordovician Period (early Hirnantian). However, after a more unified ecological regime during the latest Hirnantian Ice Age, from early Silurian to Early Devonian time, the Mediterranean Province was replaced in comparably higher-latitudes by the Malvinokaffric Province. Its distribution also reflects the fact that most of Gondwana had continuously remained over the South Pole since the Cambrian Period.

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References

- Álvaro JJ, Ferretti A, González-Gómez C, Serpagli E, Tortello MF, Vecoli M and Vizcaíno D (2007) A review of the Late Cambrian (Furongian) palaeogeography in the western Mediterranean region, NW Gondwana. *Earth-Science Reviews* **85**, 47–81.
- Andreeva ON (1960) New species of Ordovician brachiopods of the Urals and Mugodzhär. In *New Species of Ancient Plants and Invertebrates of the USSR, Part 1* (ed. BP Markovskii), pp. 286–298. Moscow: Gosudarstvennoe nauchno-tekhnicheskoe izdatelstvo literatury po geologii i okhrane nedr (in Russian).
- Bassett MG, Popov LE and Holmer LE (1999) Organophosphatic brachiopods: patterns of biodiversification and extinction in the early Palaeozoic. *Geobios* **32**, 145–63.
- Bassett MG, Popov LE and Holmer LE (2002) Brachiopods: Cambrian–Tremadoc precursors to Ordovician radiation events. In *Palaeobiology and Biodiversity Change: The Ordovician and Mesozoic–Cenozoic Radiations* (eds JA Crame and AW Owen), pp. 13–23. Geological Society of London, Special Publication no. 194.
- Bates DEB (1968) The Lower Palaeozoic brachiopod and trilobite faunas of Anglesey. *Bulletin of the British Museum (Natural History), Geology* **16**, 125–99, pls 1–14.
- Bednarczyk WS (1988) Rola brachiopodów inarticulata w stratygrafii najniższego ordowiku Gór Świętokrzyskich. *Przegląd Geologiczny* **36**, 17–23.
- Bednarczyk WS (1999) Significance of the genus *Thysanotos* Mickwitz, 1896 for the Ordovician stratigraphy of east-central Europe. *Bulletin of the Polish Academy of Sciences: Earth Sciences* **47**, 15–25.
- Benedetto JL (ed.) (2003) *Ordovician Fossils of Argentina*. Córdoba: Universidad Nacional de Córdoba, 561 pp.
- Benedetto JL (2009) *Chaniella*, a new lower Tremadocian (Ordovician) brachiopod from north-western Argentina. *Paläontologische Zeitschrift* **83**, 393–405.
- Benedetto JL and Carrasco PA (2002) Tremadoc (earliest Ordovician) brachiopods from Purmamarca and the Sierra de Mojotoro, Cordillera Oriental of northwestern Argentina. *Geobios* **35**, 647–61.
- Benedetto JL and Muñoz DF (2015) Linguloidean brachiopods from the lower Ordovician (Tremadocian) of northwestern Argentina. *Bulletin of Geosciences* **90**, 417–30.
- Benedetto JL and Muñoz DF (2017) Linguloidean brachiopods from the lower Ordovician of northwestern Argentina phylogenetic relationships with *Tarfaya* Havlíček and the origin of heterorthids. *Journal of Systematic Palaeontology* **15**, 43–67.

- Benedetto JL, Vaccari NE, Waisfeld BG, Sánchez TM and Foglia RD** (2009) Cambrian and Ordovician biogeography of the South American margin of Gondwana and accreted terranes. In *Early Palaeozoic Peri-Gondwana Terranes: New Insights from Tectonics and Biogeography* (ed. MG Bassett), pp. 201–32. Geological Society of London, Special Publication no. 325.
- Bergström SM, Chen X, Gutiérrez-Marco JC and Dronov A** (2009) The new chronostratigraphic classification of the Ordovician System and its relations to major regional series and stages and to $\delta^{13}\text{C}$ chemostratigraphy. *Lethaia* **42**, 97–107.
- Biernat G** (1973) Ordovician brachiopods from Poland and Estonia. *Palaeontologica Polonica* **28**, 1–16.
- Billings E** (1872) On some fossils from the primordial rocks of Newfoundland. *Canadian Naturalist and Geologist* (new series) **6**, 465–79.
- Budil P, Mergl M and Smutek D** (2016) Paleontologicky vyzkum lokality Brloh v Zeleznych horach (lipolické souvrství, spodní ordovik). *Zpravy o Geologických Vyzkumech* **49**, 149–56.
- Cocks LRM** (1993) Triassic pebbles, derived fossils, and the Ordovician to Devonian palaeogeography of Europe. *Journal of the Geological Society, London* **150**, 219–26.
- Cocks LRM** (2002) Key Lower Palaeozoic faunas from near the Trans-European Suture Zone. In *Palaeozoic Amalgamation of Central Europe* (eds JA Winchester, TC Pharaoh and J Verniers), pp. 37–46. Geological Society, London, Special Publication no. **201**.
- Cocks LRM and Fortey RA** (1988) Lower Palaeozoic facies and faunas around Gondwana. In *Gondwana and Tethys* (eds MG Audley-Charles and A Hallam), pp. 183–200. Geological Society of London, Special Publication no. 37.
- Cocks LRM and Fortey RA** (1990) Biogeography of Ordovician and Silurian faunas. In *Palaeozoic Palaeogeography and Biogeography* (eds WS McKerrow and CR Scotese), pp. 97–104. Geological Society of London, Memoir no. 12.
- Cocks LRM and Fortey RA** (2009) Avalonia: a long-lived terrane in the Lower Palaeozoic? In *Early Palaeozoic Peri-Gondwana Terranes: New Insights from Tectonics and Biogeography* (ed. MG Bassett), pp. 141–55. Geological Society of London, Special Publication no. 325.
- Cocks LRM and Popov LE** (2019) Early Ordovician brachiopods from southwest Wales. *Proceedings of the Geologists' Association* **130**, 677–90.
- Cocks LRM and Torsvik TH** (2013) The dynamic evolution of the Palaeozoic geography of Eastern Asia. *Earth-Science Reviews* **117**, 40–79.
- Cocks LRM and Torsvik TH** (2020) Ordovician palaeogeography and climate change. *Gondwana Research*, published online 24 October 2020, doi.org/10.1016/j.gr.2020.09.008.
- Coke C and Gutiérrez-Marco JC** (2001) Braquiópodos Linguliformes del Ordovícico Inferior de la Serra do Marão (Zona Centroibérica, N de Portugal). *Bolletín Geológico y Minero* **112**, 33–50.
- Cope JCW** (1996) Early Ordovician (Arenig) bivalves from the Llangynog Inlier, South Wales. *Palaeontology* **39**, 979–1025.
- Dean WT** (2005) Trilobites from the Çal Tepe Formation (Cambrian), near Seydişehir, Central Taurides, Southwestern Turkey. *Turkish Journal of Earth Sciences* **14**, 1–71.
- Emig CC and Gutiérrez-Marco JC** (1997) Signification des niveaux à lingulidés à la limite supérieure du Grès Armoricaïn (Ordovician, Arenig), sud-ouest de l'Europe. *Geobios* **30**, 481–95.
- Fan JX, Shen SZ, Erwin DH, Sadler PM, MacLeod N, Cheng QM, Hou XD, Yang J, Wang XD, Wang Y and Zhang H** (2020) A high-resolution summary of Cambrian to early Triassic marine invertebrate biodiversity. *Science* **367**, 272–7.
- Fortey RA and Cocks LRM** (2003) Palaeontological evidence bearing on global Ordovician–Silurian continental reconstructions. *Earth-Science Reviews* **61**, 245–307.
- Franke W, Cocks LRM and Torsvik TH** (2017) The Palaeozoic Variscan oceans revisited. *Gondwana Research* **48**, 257–84.
- Ghavidel-Syooki M, Popov LE, Alvaro JJ, Ghobadi Pour M, Tolmacheva TY and Ehsani MH** (2014) Dapingian–lower Darriwilian (Ordovician) stratigraphic gap in the Faraghan mountains, Zagros ranges, south-eastern Iran. *Bulletin of Geosciences* **89**, 679–706.
- Ghobadi Pour M, Bauert H, Popov LE, Holmer LE and Álvaro JJ** (2017) Eutrophication by biogenic phosphate pollution as a triggering factor for the collapse of oboloid-dominant brachiopod communities in the early Tremadocian of East Baltica. *61st Palaeontological Association Annual Meeting*, 7–19 December 2017, London. Palaeontological Association, Abstract Volume, pp. 108–9.
- Ghobadi Pour M, Popov LE, Kebria-Zadeh MR and Baars C** (2011) Middle Ordovician (Darriwilian) brachiopods associated with the *Nesouretus* biofacies, eastern Alborz Mountains, Iran. *Memoirs of the Association of Australasian Palaeontologists* **42**, 263–83.
- Gutiérrez-Marco JC, Sá AA, García-Bellido DC and Rábano I** (2014) The extent of the Middle Ordovician Dapingian Stage in peri-Gondwanan Europe and North Africa: stratigraphic record, biostratigraphic tools and regional chronostratigraphy. *GFF* **136**, 90–4.
- Gutiérrez-Marco JC, Robardet M, Rábano I, Sarmiento GN, San José Lancha MÁ, Herranz Araújo P and Pieren Pidal AP** (2002) Ordovician. In *The Geology of Spain* (eds W Gibbons and T Moreno), pp. 32–49. Geological Society of London.
- Gutiérrez-Marco JC and Villas E** (2007) Brachiopods from the uppermost Lower Ordovician of Peru and their palaeogeographical significance. *Acta Palaeontologica Polonica* **52**, 547–62.
- Gutiérrez-Marco JC, Yanev SN and Sachanski VV** (1999) Braquiópodos inarticulados de la Unidad Ranovac-Vlasina (“Supragethicum”) y paleobiogeografía de la unidades tectónicas balcánides de Serbia oriental (Yugoslavia). *Temas Geológico Mineros ITGE* **26**, 566–74.
- Hammer Ø and Harper DAT** (2006) *Paleontological Data Analysis*. Oxford: Blackwell.
- Hammer Ø, Harper DAT and Ryan PD** (2014) PAST: palaeontological statistics software package for education and data analysis. *Palaeontologia Electronica*, <https://palaeo-electronica.org/content/>.
- Harper DAT, Cascales-Miñana B and Servais T** (2020) Early Palaeozoic diversifications and extinctions in the marine biosphere: a continuum of change. *Geological Magazine* **157**, 5–21.
- Harper DAT, Rasmussen CMØ, Liljeroth M, Blodgett RB, Candela Y, Jin J, Percival IG, Rong JY, Villas E and Zhan RB** (2013) Biodiversity, biogeography and phylogeography of Ordovician rhynchonelliform brachiopods. In *Early Palaeozoic Biogeography and Palaeogeography* (eds DAT Harper and T Servais), pp. 127–44. Geological Society of London, Memoir no. 38.
- Harper DAT and Servais T** (eds) (2013) *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society of London, Memoir no. 38, 490 pp.
- Havlíček V** (1949) Brachiopods of the order Orthida in Czechoslovakia. *Sborník Státního geologického ústavu Československé republiky* **16**, 93–144, pls 1–5 (in Czech).
- Havlíček V** (1971) Brachiopodes de l'Ordovicien du Maroc. *Notes et Memoires du Service Géologique du Maroc* **230**, 1–135, pls 1–26.
- Havlíček V** (1977) Brachiopods of the order Orthida in Czechoslovakia. *Rozpravy Ústředního ústavu geologického* **44**, 1–327, pls 1–56.
- Havlíček V** (1980) *Inarticulate Brachiopods in the Lower Ordovician of the Montagne Noire (South France)*. Carcassonne: Mémoire de la Société des Etudes Scientifiques de l'Aude. 11 pp, pl. 1.
- Havlíček V** (1982) Lingulacea, Paterinacea, and Siphonotretacea (Brachiopoda) in the Lower Ordovician sequence of Bohemia. *Sborník geologických Věd, Geologie* **25**, 9–82, pls 1–16.
- Havlíček V** (1989) Climatic changes and development of benthic communities through the Mediterranean Ordovician. *Sborník geologických Věd, Geologie* **44**, 79–116.
- Havlíček V and Branisa L** (1980) Ordovician brachiopods of Bolivia. *Rozpravy Československé Akademie Rada Matematických a Přírodních Věd* **90**, 1–54, pls 1–6.
- Havlíček V and Josopait V** (1972) Articulate brachiopods from the Iberian Chains, northeast Spain (Middle Cambrian–Upper Cambrian–Tremadoc). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **140**(3), 328–53.
- Havlíček V and Vaněk J** (1966) The biostratigraphy of the Ordovician of Bohemia. *Sborník geologických Věd, Geologie* **8**, 7–69.

- Havlíček V, Vaněk J and Fatka L (1994) Perunica microcontinent in the Ordovician (its position within the Mediterranean Province, series division, benthic and pelagic associations). *Sborník geologických Věd, Geologie* **46**, 23–56.
- Holmer LE and Biernat G (2002) Lingulate brachiopods from Lower Ordovician (Tremadoc) chalcidites, Holy Cross Mountains, Poland. *Acta Palaeontologica Polonica* **47**, 141–56.
- Holmer LE, Popov LE, Ghobadi Pour M, Klishevich LA, Liang Y and Zhang Z (2020) Linguliform brachiopods from the Cambrian (Guzhangian) Karpinsk Formation of Novaya Zemlya. *Papers in Palaeontology* **6**, 571–92.
- Kebria-ee Zadeh M, Ghobadi Pour M, Popov LE, Baars C and Jahangir H (2015) First record of the Ordovician fauna in Mile-Kuh, eastern Alborz, northern Iran. *Estonian Journal of Earth Sciences* **64**, 121–39.
- Lavié FJ and Benedetto JL (2020) First lingulate brachiopods from the Ordovician volcano-sedimentary rocks of the Famatina Range, western Argentina. *PalZ*, published online 2019, doi:10.1007/s12542-019-00496-5.
- Legrand P (1971) A propos de la presence de *Dinobolus* (?) aff. *brimonti* (M. Rouault) au Sahara Algerien. *Mémoires du BRGM* **73**, 79–84.
- Massa D, Havlíček V and Bonnefous J (1977) Stratigraphic and faunal data on the Ordovician of the Rhadames Basin (Libya and Tunisia). *Bulletin Central de Recherches Exploration et Production Elf-Aquitaine* **1**, 3–27.
- McDougall N, Brenchley PJ, Rebelo JA and Romano M (1987) Fans and fan deltas – precursors to the Armorican Quartzite (Ordovician) in western Iberia. *Geological Magazine* **134**, 347–59.
- Mélou M (1982) Brachiopodes articulés. *Mémoire de la Société des Etudes Scientifiques de l'Aude*, 23–35, pls 1–7.
- Mergl M (1981) The genus *Orbithele* (Brachiopoda, Inarticulata) from the Lower Ordovician of Bohemia and Morocco. *Věstník Ústředního ústavu geologického* **56**, 287–292.
- Mergl M (1983) New brachiopods (Cambrian-Ordovician) from Algeria and Morocco (Mediterranean Province). *Časopis pro Mineralogii a Geologii* **28**, 337–48.
- Mergl M (1984) Fauna of the Upper Tremadocian of Central Bohemia. *Sborník geologických Věd, Paleontologie* **26**, 9–46.
- Mergl M (1995) New lingulate brachiopods from the Mílina Formation and the base of the Klabava Formation (late Tremadoc – early Arenig), Central Bohemia. *Věstník Českého geologického ústavu* **70**, 101–14, pls 1–4.
- Mergl M (1997) Distribution of the lingulate brachiopod *Thysanotos* in Central Europe. *Věstník Českého geologického ústavu* **72**, 27–35.
- Mergl M (2002) Linguliform and craniiform 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 (2011) Reassessment of the Ordovician brachiopod *Poramborthis* and *Poramborthidae*. *Memoirs of the Association of Australasian Palaeontologists* **41**, 351–358.
- Muñoz DF and Benedetto JL (2016) The eorthisid brachiopod *Apheorthis* in the Lower Ordovician of NW Argentina and the dispersal pathways along western Gondwana. *Acta Palaeontologica Polonica* **61**, 633–44.
- Nasedkina VA (1977) On the Ordovician brachiopods from the Chaushka river basin in northern Mugodzhary. In *Materialy po paleontologii srednego paleozoya Urala i Sibiri* (eds VP Sapelnikov and BI Chuvashov). Trudy Instituta geologii i geokhimii, Akademiya Nauk SSSR, Uralskii Nauchnyi Tsentr 126, 11–23 (in Russian).
- Neuman RB and Bates DEB (1978) Reassessment of Arenig and Llanvirn age (early Ordovician) brachiopods from Anglesey, north-west Wales. *Palaeontology* **21**, 571–613, pls 63–68.
- Popov LE and Cocks LRM (2017) The World's second oldest strophomenoid-dominated benthic assemblage in the first Dapingian (Middle Ordovician) brachiopod fauna identified from Iran. *Journal of Asian Earth Sciences* **140**, 1–12.
- Popov LE, Ghobadi Pour M, Bassett MG and Kebria-Ee M (2009) Billingsellide and orthide brachiopods: new insights into earliest Ordovician evolution and biogeography from northern Iran. *Palaeontology* **52**, 35–52.
- Popov LE, Ghobadi Pour M and Hosseini M (2008) Early to Middle Ordovician lingulate brachiopods from the Lashkarak Formation, Eastern Alborz Mountains, Iran. *Alcheringa* **32**, 1–35.
- Popov LE and Holmer LE (1994) Cambrian-Ordovician lingulate brachiopods from Scandinavia, Kazakhstan, and South Ural Mountains. *Fossils & Strata* **35**, 1–156.
- Popov LE, Holmer LE, Bassett MG, Pour MG and Percival IG (2013a) Biogeography of Ordovician linguliform and craniiform brachiopods. In *Early Palaeozoic Biogeography and Palaeogeography* (eds DAT Harper and T Servais), pp. 117–26. Geological Society of London, Memoir no. 38.
- Popov LE, Kebria-Ee Zadeh M-R, Ghobadi Pour M, Holmer LE and Modzalevskaya TL (2013b) Cambrian (Furongian) rhynchonelliform brachiopods from the Eastern Alborz Mountains, Iran. *Bulletin of Geosciences* **88**, 525–38.
- Popov LE, Khazanovitch KK, Borovko NG, Sergeeva SP and Sobolevskaya RF (1989) The key sections and stratigraphy of the Cambrian-Ordovician phosphate-bearing obolus beds on the north-eastern Russian platform. *Ministerstvo Geologii SSSR, Mezhdovedstvennyi stratigraficheskij komitet SSSR, Trudy* **18**, 1–222.
- Popov LE, Legrand P, Bouterfa B and Ghobadi Pour M (2019) Ordovician cold water brachiopods from the Ougarta Mountain Range, Algerian Sahara. *Bulletin of Geosciences* **94**, 41–70.
- Popov LE, Vinn O and Nikitina OI (2001) Brachiopods of the redefined family Tritoechiidae from the Ordovician of Kazakhstan and South Urals. *Geobios* **32**, 131–55.
- Rouault M (1850) Note préliminaire sur une nouvelle formation découverte dans le terrain Silurien de la Bretagne. *Bulletin de la Société Géologique de France (Series 2)* **7**, 724–44.
- Rubel M (1964) Lower Ordovician brachiopods of the superfamilies Orthacea, Dalmanellacea and Syntrophicea of the Eastern Baltic. *Eesti NSV Teaduste Akademia Geologia Instituudi Uurimused* **6**, 141–224 (in Russian).
- Sdzuy K (1955) Die Fauna der Leimitz-Schiefer (Tremadoc). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* **492**, 1–74.
- Sdzuy K, Hammann W and Villas E (2001) The upper Tremadoc fauna from Vogtendorf and the Bavarian Ordovician of the Frankenwald (Germany). *Senckenbergiana lethaea* **81**, 207–61.
- Spjeldnaes N (1961) Ordovician climatic zones. *Norsk Geologisk Tidsskrift* **41**, 45–77.
- Streng M, Mellbin BB, Landing E and Keppie JD (2011) Linguliform brachiopods from the terminal Cambrian and lowest Ordovician of the Oaxaquia Microcontinent (Southern Mexico). *Journal of Paleontology* **85**, 122–55.
- Sturesson ULF, Popov LE, Holmer LE, Bassett MG, Felitsyn S and Belyatsky B (2005) Neodymium isotopic composition of Cambrian–Ordovician biogenic apatite in the Baltoscandian Basin: implications for palaeogeographical evolution and patterns of biodiversity. *Geological Magazine* **142**, 419–39.
- Sutton MD, Bassett MG and Cherns L (1999, 2000) Lingulate brachiopods from the Lower Ordovician of the Anglo-Welsh Basin. *Monograph of the Palaeontographical Society, London*, Part 1, **153**, 1–60, pls 1–8; Part 2, **154**, 61–114, pls 9–23.
- Torsvik TH and Cocks LRM (2011) The Palaeozoic geography of central Gondwana. In *The Formation and Evolution of Africa: A Synopsis of 3.8 Ga of Earth History* (eds DJJ van Hinsbergen, SJH Buiter, TH Torsvik, C Gaina and SJ Webb), pp. 137–66. Geological Society of London, Special Publication no. 357.
- Torsvik TH and Cocks LRM (2017) *Earth History and Palaeogeography*. Cambridge: Cambridge University Press, 317 pp.
- Traynor JJ (1988) The Arenig in South Wales: sedimentary and volcanic processes during the initiation of a marginal basin. *Geological Journal* **23**, 275–92.
- Ulrich EO and Cooper GA (1938) Ozarkian and Canadian Brachiopods. *Geological Society of America Special Paper* **13**, 1–323, pls 1–58.
- Videt B, Paris F, Rubino JL, Boumendjel K, Dabard MP, Loi A, Ghienne JF, Marante A and Gorini A (2010) Biostratigraphical calibration of third order Ordovician sequences on the northern Gondwana platform. *Palaeogeography, Palaeoclimatology, Palaeoecology* **296**, 359–75.
- Villas E (1995) Caradoc through early Ashgill Brachiopoda from the Central-Iberian Zone (Central Spain). *Geobios* **38**, 49–84.

- Villas E, Herrera ZA and Ortega GC** (2009) Early orthid brachiopods from the Tremadocian (Lower Ordovician) of northwestern Argentina. *Journal of Paleontology* **83**, 604–13.
- Vizcaíno D, Álvaro JJ and LeFebvre B** (2001) The Lower Ordovician of the southern Montagne Noire. *Annales Société Géologique du Nord* **8**, 213–20.
- Webby BD, Paris F, Droser ML and Percival IG** (eds) (2004) *The Great Ordovician Biodiversification Event*. New York: Columbia University Press, 484 pp.
- Williams A** (1974) Ordovician Brachiopoda from the Shelve District, Shropshire. *Bulletin of the British Museum (Natural History), Geology, Supplement* **11**, 1–163, pls 1–28.
- Zhan R and Jin J** (2014) Early–Middle Ordovician brachiopod dispersal patterns in South China. *Integrative Zoology* **9**, 121–40.
- Ziegler AM, Cocks LRM and Bambach RK** (1968) The composition and structure of Lower Silurian marine communities. *Lethaia* **1**, 1–27.