

Faunal dynamics between Iberia and Bohemia during the Oretanian and Dobrotivian (late Middle-earliest Upper Ordovician), and biogeographic relations with Avalonia and Baltica

Juan C. GUTIÉRREZ-MARCO¹⁾, Isabel RÁBANO²⁾, Graciela N. SARMIENTO¹⁾, Guillermo F. ACEÑOLAZA³⁾, Miguel A. SAN JOSÉ¹⁾, Agustín P. PIEREN¹⁾, Pedro HERRANZ¹⁾, Helena M. COUTO⁴⁾, José M. PIÇARRA⁵⁾

¹⁾ Instituto de Geología Económica (CSIC-UCM), Facultad de Ciencias Geológicas, 28040 Madrid, Spain

²⁾ Museo Geominero, ITGE, Ríos Rosas 23, 28003 Madrid, Spain

³⁾ Instituto Sup. Correlación Geológica, CONICET-Fac. CC. Naturales e IML-UNT, Miguel Lillo 205, 4000 Tucumán, Argentina

⁴⁾ Centro de Geologia da Universidade do Porto e Faculdade de Ciências, Pça. Gomes Teixeira, 4050 Porto, Portugal

⁵⁾ Instituto Geológico e Mineiro, Ap. 104, 7802 Beja Codex, Portugal

Increasing paleomagnetic empiricism, and the spread of 'terrane possibilities' for paleogeographic reconstructions among authors from many different fields, have led during the last years towards a progressive splitting of the so-called 'Armorican terrane family', that lied along the northern margin of the Gondwanan continent during the Lower Paleozoic times. As a result, there is a confusing melange of European 'platelets' between the stable plates of Baltica and African Gondwana, arranged in different ways according to each of the multiple proposals. These are often in flagrant contradiction with the most elementary sedimentary evidences, and especially with the verdict provided by the paleontological record from equivalent paleoenvironments.

The best preserved and significant parts of this mosaic are the large Hesperian Massif of Iberia, the Armorican Massif, and the Barrandian area, which during the last decade have suffered different stages of 'divorce' and further 'reconciliation' promoted by paleomagneticians. Once the 'adventure' that made the actual Perunica abandon Gondwana towards intermediate paleolatitudes has been overcome, it now just seems to be separated from Ibero-Armorica by a 'Sardinian-Taurian' rise, uplifted in Middle Ordovician times as a consequence of the 'Sardic movements'. The relative west-east alignment of these three areas along the North Gondwanan margin has become progressively clearer to us on the basis of the faunal and sedimentary evidence: an inverted Armorican Massif was situated in prolongation with the Central Iberian Zone, and both were parts of a single segment of the shallow shelf surrounding Gondwana. Perunica lied to the east of this Ibero-Armorican Domain, but there are not still enough data for a precise determination of their exact position.

The aim of this contribution is to shed some light about these relationships based on the Middle Ordovician faunal dynamic patterns. The development of a regional chronostratigraphic scale for the Mediterranean area

allowed us to establish very precise biochronological subdivisions for the Oretanian and Dobrotivian, which can be applied for the correlation between Iberia and Bohemia. The biogeographic relationships of Bohemia with the Hesperian and Armorican massifs were already known in the middle of the XIX century. Since then, a two-way faunal exchange was assumed to exist between Bohemia and Iberia. This would imply a prime geographic continuity, and the faunal differences could be explained in terms of bathymetric biofacies. These, for instance, prevented the dispersal of the inshore *Neseuretus* Fauna into the substantially deeper Bohemian environments dominated by atheloptic communities. However, this northern Gondwanan paleobiogeographic scenario was geodynamically more complex, and rejects a direct continuity between Iberia and Bohemia. This scenario was later obscured and overprinted by Variscan tectonics. A more precise analysis of the synchronicity or diachroneity of the Ibero-Bohemian shared paleontological record allows to understand and elucidate some of these paleobiogeographic relations.

The chronostratigraphic range of our observations is basically referred to the mid to upper Darriwilian global Stage of the Middle Ordovician Series. In terms of the Mediterranean scheme, it is equivalent to the Oretanian and Dobrotivian (*p.p.*) regional stages. The latter includes the limit with the Upper Ordovician, indirectly correlated with the first record of a graptolite never found in the North Gondwanan realm.

EARLY FAUNAL LINKS

Simultaneous record of significant benthic faunas in Bohemia and Central Iberia during the Oretanian age is exemplified by the common occurrence of trilobites [*Placoparia* (*P.*) *cambriensis* Hicks (= *Placoparia barrandei* Prantl et Šnajdr), *Hungioides bohemicus*

(Klouček), *Selenopeltis macrophtalma* (Klouček)], bivalves [*Babinka prima* Barrande, *Redonia deshayesi* Rouault (= *R. bohémica* Barrande), *Coxiconchia britannica* (Rouault) s.str. (= *C. b. holubi* Kříž)], etc., or by the trilobite genera *Asaphellus*, *Bathycheilus*, *Colpocoryphe*, *Ectillaenus*, *Nobiliasaphus*, *Dionide*, *Geragnostus* or *Uralichas*. Most of these faunas were previously recorded in the Arenig of Eastern Avalonia, SW France and the North African and South American margins of Gondwana, and on the shallowest areas of Iberia (directly above the Armorican Quartzite facies) as a consequence of the global 'Llanvirn transgression'. The rapid dissipation of its influx promotes the appearance of other strongly endemic faunas (broadly designated as 'dalmanitid-calymenacean' faunas) in these high paleolatitude shelves. The Iberian record of genera such as *Bathycheilus*, *Hungioides*, *Asaphellus*, *Ogyginus*, *Toletanaspis*, *Babinka*, *Tolmachovia*, *Ekaterodonta*, *Plumulites*, *Monobolina*, thick-ribbed brachiopods, etc., is virtually restricted to the lower Oretanian. The same situation is observed with other less frequent epipelagic graptolites, some in common with Bohemia [*D. (?Corymbograptus) retroflexus* Perner and *Acrograptus lipoldi* Bouček], as well as with the youngest mediterranean representatives of the horizontal didymograptids and xiphograptids, and the biserial stock.

The existence of geographical subspecies derived from a common ancestor in the transgressive environments is exemplified by the Oretanian ophiuroids *Palaeura neglecta neglecta* Schuchert (Bohemia: non *P. n. 'bohémica'* Smith) and *P. neglecta hispanica* Smith (Central Spain).

ATHELOPTIC FAUNAS

The Iberian record of Ordovician atheloptic communities has been only recognized in the Ossa Morena Zone of SW Hesperian Massif, where cyclopygid trilobites occur during latest Tremadoc and mid Ashgill times. Similar biofacies have also been sporadically noted in the Oretanian. The latter occurrence is restricted to a single locality north of Seville, where recent research yielded some trilobites and echinoderms recorded only in Bohemia and in the Ancenis Syncline of the South Armorican Massif [*Kodymaspis puer* (Barrande), *Nerudaspis cf. aliena* (Barrande), *Ormathops* sp., *Lagynocystis pyramidalis* (Barrande), and *Plasia cf. nobilis* Prokop, a.o.]. Further confirmation of these biogeographic affinities is provided by the hyoliths, but some taxa appear earlier than in Bohemia, such as *Leolites* sp., the oldest known representative of the genus, and also *Andalucilites (nom. nud.)*, probably related to the younger Bohemian species *Carinolites? tantulus* (Marek). Besides these genera, the rare findings of *Cavernolites* sp. and *Pauxillites* sp., both of presumed Moroccan origin, seem to indicate a simultaneous migration reaching Iberia and Bohemia during the Oretanian. However, the faunal exchange among the atheloptic faunas of Bohemia and Ibero-Armorica is of rather limited significance, due to the dissimilar diversity shown by the Oretanian occurrences of true Bohemian faunas in SW Europe. Moreover, the

concurrency of *Salterocoryphe* n.sp. and *Tolmachovia* n.sp. in the Ossa Morena Zone (both unknown in Bohemia) demonstrates the influence of local migrations from the Arenig of SW France during the 'Llanvirn transgression', as also displayed by coeval faunas in the relatively deeper parts of the Central Iberian shelf. Furthermore, the presence of the trilobite *Selenopeltis buchi* (Barrande) s.str., from Oretanian nodules of the Ossa Morena Zone, is equated with its occurrence in the early Abereiddian of Britain, whereas in Bohemia this species starts in the Berounian (Letná Fm.). The presence of *Euorthisina* sp. in the Iberian assemblage is also demonstrative of the Oretanian spreading of this genus of South American origin in deep water facies of northern Gondwana.

The Ossa Morena Zone of southwestern Iberia does not show relations with any internal North Gondwanan seaway (i.e., the 'Nantes-Sardic Line'), and most probably represents an exotic terrane accreted to the western part of the external margin of the Iberian shelf during the Cadomian Orogeny. Later reactivation along the Cadomian sutures in Paleozoic times ends with its juxtaposition on the much more internal blocks of the Hesperian Massif.

IBERIAN IMMIGRANTS TO BOHEMIA

The chronostratigraphic refinement achieved with the Mediterranean regional scheme for the Middle and Upper Ordovician, allowed to recognize diachronism in the first appearance of some benthic to epiplanktic taxa common to Iberia and Bohemia. By the end of the Arenig, the enhancement of generic and even species similarity between the Oretanian faunas of both areas may be partly due to the coeval "Llanvirn transgression", as exemplified by the above mentioned taxa (*Babinka*, *Hungioides*, *Lagynocystis*, etc.). However, and after finishing its influx, a one-way migration route was established from the west to the east, as indicated by common taxa always appearing earlier in Iberia than in Bohemia.

A high resolution biostratigraphy of the Bohemian benthic fossils has not been developed. Therefore, here we will only mention those migrations detected at the level of regional stages. The most significant patterns were recognized among taxa from the Iberian Oretanian, whose first appearance in Bohemia took place in the Dobrotivian, and that of the Oretanian or Dobrotivian Iberian taxa which delay their presence in Bohemia until the Berounian.

The first example is the epiplanktic orthid *Brandysia cf. benigna* Havlíček, from the latest Oretanian of N Spain: the nominal species is a very typical element of the *Paterula circina* community of the Bohemian Dobrotivian. A second one is the bivalve *Praeleda costae* (Sharpe), whose first occurrence is in the lower Oretanian of Spain, and which is possibly recorded in the Bohemian Dobrotivian (as "*Leda bohémica*" sensu Barrande p.p., fide Pfab). The FAD of *Colpocoryphe grandis* (Šnajdr) is probably located in the Oretanian of NW Spain, reaching Bohemia during the Dobrotivian. Among the pelagic ostracods, the latest Oretanian appearance of *Quadritia (Krutatia) tromelini* Vannier et Schallreuter in north Spain

slightly precedes its first record in Bohemia (basal Dobrotivian). The Berounian brachiopod genus *Jezerzia* is first recorded in northern Spain during the latest Dobrotivian. The trilobite genera *Zeliszella* (Z.) and *Eccoptochile*, and perhaps also *Prionocheilus mendax* (Vaněk), seem to have migrated from Iberia to Bohemia by the early Dobrotivian. All three taxa have been recorded in Iberia starting from the late Oretanian, but their origin lies in other peri-Gondwanan areas (Morocco, the Tarim Basin and Wales, respectively) as early as in the late Arenig (*Eccoptochile*, *P. mendax*). The brachiopod genus *Aegiromena*, coming from the South American peri-Gondwana, as the kerformellinid trilobites, migrated to Iberia in the Dobrotivian, and its appearance in Bohemia, somewhat delayed, serves to characterize the local base of the type Berounian.

The most remarkable group of taxa among the common Ibero-Bohemian elements is composed of those Oretanian-Dobrotivian species which arrive to Bohemia in the Berounian, such as *Myoplusia bilunata perdentata* (Barrande): upper Oretanian to upper Dobrotivian and undetermined Berounian of Spain, Berounian (Bohdalec Fm.) to Králodvorian in Bohemia; *Technophorus sharpei* (Barrande): lower Oretanian in Spain, Berounian (Vinice Fm.) to Králodvorian in Bohemia; *Aristocystites metroi* Parsley et Prokop: lower Dobrotivian in Spain, Berounian (Zahořany Fm.) to Kosovian in Bohemia; *Aristocystites bohemicus* Barrande: upper Oretanian in Morocco, Dobrotivian in Spain, Berounian in Bohemia (Vinice and Zahořany fms.); *Codiacystis moneta* (Barrande) *s.l.* and *C. aff. bohémica* (Barrande), lower Dobrotivian in Spain vs. Berounian (Zahořany Fm.) in Bohemia and Lybia (*C. bohémica*). Besides these molluscan and echinoderm species, the hyolith genera *Leolites*, *Andalucilites* and *Recilites*, first recorded in the Iberian Oretanian, have their FADs in Bohemia during the Berounian (Liben and Vinice fms.). The typical Berounian brachiopod *Drabovia* appeared in Central Spain as early as in the early Oretanian (*D. praedux* Havlíček, stratotype revised by JCG-M). Finally, the asaphid trilobite *Nobiliasaphus nobilis* (Barrande) *s.l.*, whose evolutive lineage started in the late Oretanian of Spain (very large representatives of the species occur in the late early Dobrotivian), delays its first appearance in Bohemia and ?Turkey up to the Berounian (Vinice and ?Bedinan fms.).

A last grouping of common taxa between Iberia and Bohemia is represented by some Dobrotivian species which are roughly coeval in both areas. These are the benthic trilobites *Placoparia* (*Coplacoparia*) *borni* Hammann [= *P. (C.) antiopa* Moravec, *vide* Havlíček and Vaněk], *Eccoptochile mariana* Verneuil et Barrande [= *E. vipera* Moravec, *vide* Havlíček and Vaněk], both recorded from the late Dobrotivian, the nektobenthic *Parabarrandia crassa* (Barrande), sporadically recognized (with very large specimens) in some late early Dobrotivian localities of Spain and Portugal, and the diploporid *Calix purkynei* (Klouček), which occurs in the basal Dobrotivian of Spain, as well as in a single Bohemian locality of the Skalka facies (Dobrotivian).

Other Spanish taxa also recognized in Bohemia, such as *Bathmoceras cf. praeposterum* Barrande, *Tropidodiscus pusillus* (Barrande in Perner), *Archinacella ovata* Barrande in Perner, *Ptychonema*, *Pygmaeoconus*, *Bactrotheca*, *Gompholites*, etc., are not considered here because of insufficient biostratigraphic control. However, none of these forms would exchanges.

AVALONIAN IMMIGRANTS

The overall drop of generic similarity observed during the Oretanian and Berounian among the benthic faunas of Avalonia and the Ibero-Armorican Domain, agrees with the claimed separation and drifting of this microcontinent away from Gondwana after the early Ordovician. Sudden appearance of Avalonian taxa in Iberia is rather anecdotic and was noticed, for instance, by the record of typical trilobite genera like *Protolloydolithus* (so far restricted to the British Abereiddian) in the upper lower Dobrotivian of north Portugal, and *Myttonia* (Moridunian of south Britain) in the upper Dobrotivian of central Spain. A similar diachroneity was observed with other Iberian records of the brachiopod species *Gelidorthis cennenensis* Lockley et Williams (upper lower Abereiddian in Britain) and *Dalmanella parva* Williams (upper lower Abereiddian to Aurelucian), both associated to *Myttonia* in the Spanish Dobrotivian. Scattered occurrences of other brachiopod genera, such as *Macrocoelia*, *Salopia*, *Mcewanella* or *Porambonites*, confirm this episodic Avalonian influx into Iberia during the Oretanian and Dobrotivian. None of the above mentioned taxa occurred in the coeval Bohemian assemblages. Finally, some taxa originary from the South American Arenig, such as *Euorthisina*, *Aegiromena* and *Tissintia*, first arrived to Avalonia and N Africa during the Abereiddian-Oretanian, and from there migrated to Ibero-Armorica and Bohemia near the Oretanian/Dobrotivian boundary. The trilobite genus *Marrolithus* is another Avalonian trinucleid (first recorded in the Abereiddian of south Britain) that migrates into the Ibero-Armorican Domain by the late Dobrotivian, on its way to Bohemia (where its first occurrence is in the Berounian Vinice Fm.).

THE "BALTIC CONNECTION"

The sporadic record of some allegedly 'Baltic' genera of ostracods, conodonts and trilobites seems to occur repeatedly in the Middle Ordovician of the Ibero-Armorican Domain. However, a more detailed biochronostratigraphic analysis shows that most of these occurrences are in fact taxa which first appeared in peri-Gondwana, and from there migrated to lower paleolatitudes as far as the Baltic continental plate. The confusion arises when genera first described from Baltoscandian areas, but of peri-Gondwanan origin, like the binodicope ostracodes *Klimphores*, *Aechmina*, *Laterophores*, *Vogdesella*, and the paleocopid subgenus *Quadrilitia* (*Krutatia*), later underwent a rich adaptative radiation in Baltica during the latest-Middle and Upper

Ordovician. The same is true for some Middle Ordovician 'Baltic' conodont assemblages of Gondwana, and also for certain 'Baltic' trilobites like *Panderia*. This genus is already present in the early Darriwilian of southern Turkey, but a giant and remarkable species [*P. beaumonti* (Rouault)] has been widely recorded from the upper lower Dobrotivian to uppermost Dobrotivian in Ibero-Armorica (the genus is also recognized from the Vinician of Portugal). The alleged 'Baltic' graptolite *Gymnograptus linnarssoni* (Moberg), and its closely allied form *G. retusus* (Lapworth), displayed a widespread distribution along the margins of Gondwana, Avalonia and Baltica, being of interest for the general correlation of the lower Dobrotivian, but not for detailed biogeographic purposes.

As far as we know, the only true Baltic immigrants from the Middle Ordovician of Iberia were some tarphycerid nautiloids like *Trocholites* cf. *depressus* (Eichwald), from the early Dobrotivian of the Central Iberian Zone, which was a nectic form of temperate waters lacking pelagic larvae. The paleocopid ostracod *Ogmoopsis* (*Quadridigitalis*), of clear Baltic origins, also migrated to north Iberia by the late Oretanian, where it reached its higher abundance and diversity by the Dobrotivian. Among the Oretanian graptolites, we add the recent discovery of the Baltic species *Pseudamplexograptus distichus* (Eichwald), together with *Eoglyptograptus*, *Proclimacograptus* and *Didymograptus* (*D.*) *murchisoni* (Beck), from a latest Oretanian assemblage from northern Spain. Even if the former graptolite species takes priority over its possible synonym "*Diplograptus*" *priscus* (Elles et Wood), from the late Abereiddian of Britain, this record is of importance for the general correlation between the regional stages of Baltica, Avalonia and northern Gondwana, although the species has not yet been recorded from Bohemia. A last Baltic immigrant is the graptolite *Oepikograptus bekkeri* (Öpik) (= *Climacograptus haljalensis* Bulman), found in the terminal Dobrotivian of Spain, and also in the basal Berounian of Portugal and ?Syria (as *Diplograptus spinulosus* Sudbury, also listed from coeval Chinese beds). The vertical range of this species is considered to be equivalent to the *Nemagraptus gracilis* biozone of Scandinavia (Kukrusian stage), and thus provides a good argument to correlate the boundary between the Middle and Upper Ordovician series within the uppermost Dobrotivian stage of the Mediterranean scale.

The shift in planktic and epiplanktic Baltic faunas into Gondwana was probably linked to accidental displacement of surface water masses during extended climatic disturbances coincident with some regressive pulses. An anti-clockwise current, favoured by a sudden influence of the middle latitude atmospheric cell, also prevents the direct arrival of Baltic immigrants into Bohemia, where the Dobrotivian has been considered a time of maximum

isolation from Baltica. However, some Bohemian emigrants to Baltica could have benefitted of these currents in epochs of strong atmospheric activation, as for instance the 'Baltic' ostracod genera *Euprimites* and *Piretia*, which first occur in the basal Dobrotivian of Bohemia.

IBERO-BOHEMIAN VINICIAN FAUNAS

The earlier Berounian is badly represented in the Iberian successions, where the Dobrotivian-Berounian boundary is marked by the sudden disappearance of *Neseuretus* and by the first record of *Dalmanitina* and some endemic species of *Crozonaspis*. The regional equivalents of the Vinician substage, including the basal Zdice-Nuče iron ore horizon, are normally successions of transgressive nature that seal a basal stratigraphic gap of variable amplitude. Spanish Vinician faunas share many coeval Bohemian taxa, mostly recorded for the first time from the Liben and Letná fms., such as the gastropods *Holopea? antiquata* (Barrande in Perner) and *Nonorios pater* (Barrande in Perner), the pelmatozoans *Heliocrinites helmhackeri* (Barrande) and *Rhombifera bohémica* Barrande, or the brachiopods *Jezerzia chrustenicensis* (Havlíček), *Rafinesquina* cf. *pseudoloricata* Barrande (which appeared slightly earlier in Spain), *Rostricellula ambigena* (Barrande), *Aegiromena aquila* (Barrande) s.l., as well as other closely related species of *Gelidorthis*, *Saukrodictya*, *Drabovia*, *Prionocheilus*, *Zetillaenus*, *Actinopeltis*, *Mespilocystites*, etc.

Most of these taxa illustrate a two-way faunal exchange, occurring westwards for the above mentioned taxa (the *Drabovia* fauna also reached Avalonia by the same epoch), and eastwards for the older Ibero-Armorican stock, the latter comprising common species of the genera *Aristocystites*, *Codiacystis*, *Myoplusia*, *Technophorus*, *Nobiliasaphus*, etc. This 'breakdown' of intraprovincial differentiation can be explained by the disappearance of the main paleogeographic barrier (the Sardinian-Taurian rise) which divided the Mediterranean area starting from the Oretanian. Iberian migrations to Bohemia by the late Oretanian and Dobrotivian crossed the submerged prolongation of this barrier through the western end of the Cantabro-Ebroian Massif, whereas the eastern emerged areas retained and prevented the dispersal of many faunas until the Vinician breakdown.

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