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First Perigondwanan record of actinolepids (Vertebrata: Placodermi: Arthrodira) from the Lochkovian (Early Devonian) of Spain and its palaeobiogeographic significance

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ABSTRACT

Different palaeogeographic models have been proposed for the position of Laurussia (including Baltica) and Gondwana-derived microcontinents (including Ibero-Armorica) during Ordovician to Late Carboniferous times. Principal differences concern the presence and duration of a large ocean, the Rheic Ocean, acting as a faunal barrier between these areas. The timing of the collision of Laurussia with Gondwana and/or Gondwana-derived terranes continues to be debated. Here we present new faunal data revealing close biogeographical relations between Ibero-Armorica ("Perigondwanan" or Gondwanan derivate terranes) and Podolia (SE margin of Baltica, in Laurussia). The placoderm assemblage found in the mid-late Lochkovian (Lower Devonian) of Celtiberia (north-central Spain), consisting of the 'actinolepid' species *Kujdanowiaspis podolica*, *Erikaspis zychi* and the acanthothoracid *Palaeacanthaspis* aff. *P. vasta*, is similar, both in terms of taxonomy and stratigraphic record, to that encountered in the Lochkovian of Podolia (Ukraine; Laurussia) and until now considered as endemic to this region. Moreover, vertebrate faunal links between Podolia and Celtiberia are also extended to the chondrichthyan scale-based species *Seretolepis elegans* and *Altholepis composita* previously documented exclusively from Laurussian localities (Podolia and Mackenzie Mountains in Canada), which occur together with the placoderm remains described herein. These evidences support the hypothesis that intermittent shallow neritic migration paths between Podolia (as well as "Avalonia") and Iberia existed in the late Lochkovian, agreeing with a palaeogeographic reconstruction showing close proximity between peri-Gondwanan or Gondwana-derived terranes and Laurussia. It supports the palaeogeographic model of the non-oceanic Variscan Mobile Crustal Field and it corroborates the arguments against wide oceans, acting as biogeographical relevant barriers, between Baltica and Gondwana in early Devonian times. The distribution patterns of heavy-shelled ostracods, turbidicolous brachiopods, and Rhenish trilobites also support these conclusions.

1. Introduction

The Axial Depression of Río Cámaras (hereafter abbreviated ADRC), located in the south-eastern part of the Iberian Chains, is one of the eight areas with Devonian outcrops recognised in Celtiberia by Carls (1999; Fig. 1A and B). The ADRC exposes outcrops of marine sediments, mainly with shallow neritic facies, from the Upper Silurian, Lower Devonian (almost complete) and parts of the Middle and Late Devonian. Palaeontological studies had been carried out in the ADRC for more than one century (for a historical review, see Carls, 1999). As a result, lithostratigraphy, fossil contents and palaeoecological conditions are well known (Carls, 1988), providing, together with sedimentology, solid information on bathymetry, hydroenergy, stability of substrate and suspended matter (Dojen, 2005). In addition, conodont and invertebrate successions allow accurate biostratigraphic correlations with other regions in Europe and North Africa (Carls, 1987,1988,1996; Carls and Valenzuela-Ríos, 1998; Carls, 1999; Carls and Valenzuela Ríos, 1999). All these form a useful detailed framework for the study of early vertebrates (Mader, 1986; Wang, 1993; Botella and Valenzuela Ríos, 2005; Botella et al., 2006).

Placoderms ("armoured fishes") have been known for a long time to occur in ADRC; however, only a few of their remains have been studied. A right marginal plate of *Tityosteus* cf. *rieversae* (Arthrodira) from the lower Emsian (Mark-Kurik and Carls, 2004) and an almost complete skull roof of the arthrodire *Carolowilhelmina geognostica* from the upper Eifelian (Mark-Kurik and Carls, 2002) have been described. The presence of material belonging to Actinolepidoidei (a basal group of the Arthrodira; Dupret, 2004; Dupret et al., 2007; Dupret and Zhu, 2008;

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Dupret et al., 2009) has been briefly mentioned by Wang (1993) and by Carls (1999) but it has never been studied in detail. Here we present a systematic study of these Actinolepidoidei and other placoderm remains from the Lower Devonian of the ADRC and discuss their biostratigraphical and palaeogeographical implications.

2. Geological setting, localities and horizon

The material studied herein was collected by P. C. during palaeontological fieldwork in Celtiberia over the last few decades. It comes from outcrops of the Nogueras Formation (Lochkovian–Pragian) in two localities (Los Poyales and Mariplό) of the ADRC (Fig. 1B). The locality Los Poyales is situated between the villages of Nogueras and Santa Cruz de Nogueras, at the south slope of the mountain Valdespaña (Fig. 1C). It comprises five trenches, of which the one furthest to the southeast produces fish remains from several beds belonging to unit d2aβ5 of the Nogueras Formation. The age of this unit is middle Late Lochkovian (Fig. 2). The locality Mariplό is situated about 1.5 km NW of Santa Cruz de Nogueras and 3 km WSW of Nogueras (Fig. 1C), where a trench was dug. Near the northern

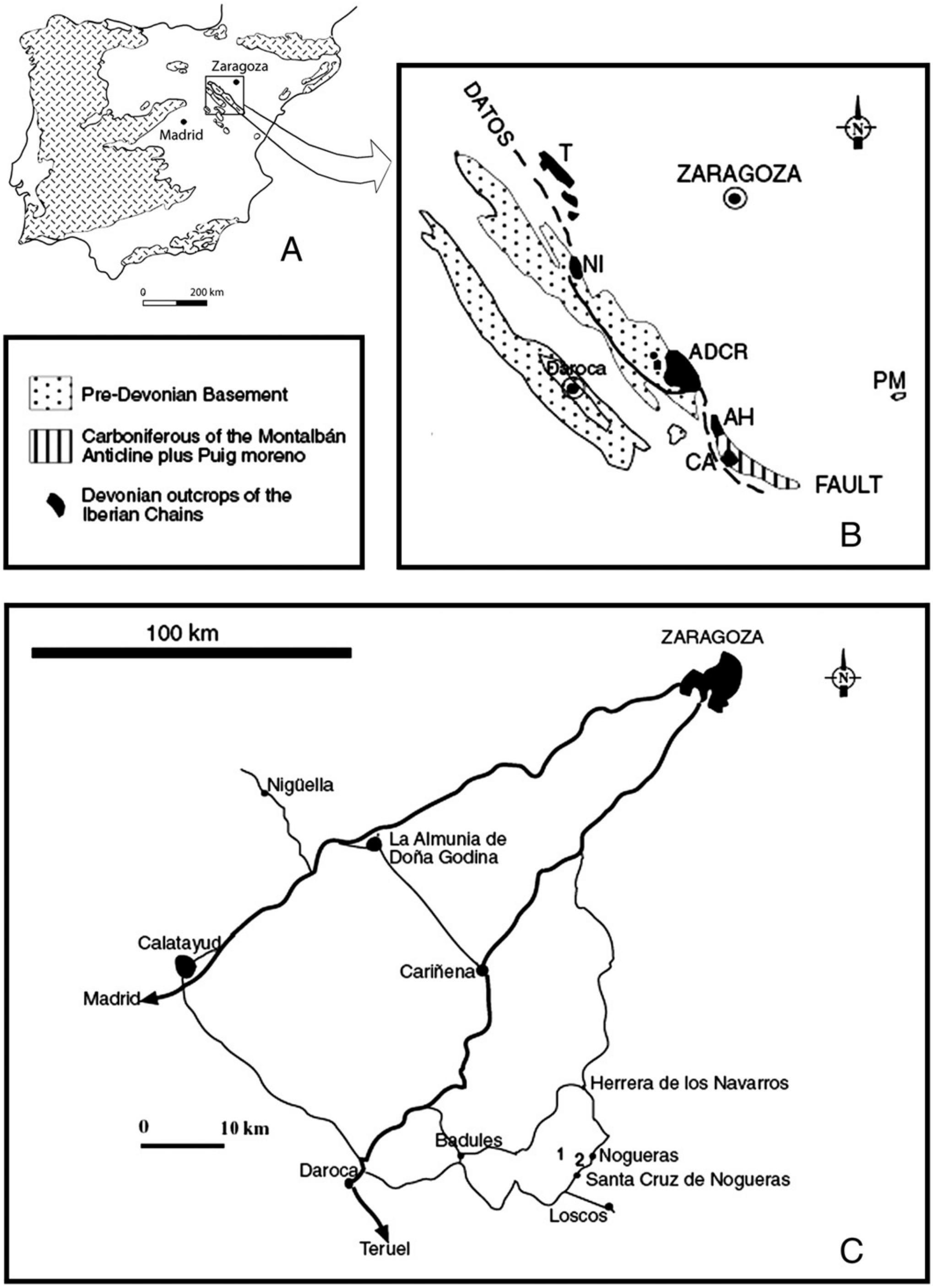

Fig. 1. A. General map of the Iberian Peninsula showing distribution of Precambrian and Palaeozoic rocks (hatched pattern) and location of Celtiberia (grey rectangle). B. Simplified geological map of Celtiberia showing the areas with Devonian outcrops (ADRC, Axial Depression of the Cámaras River; AH, Anadón–Huesa Devonian outcrops in the Montalbán Anticline; CA, Cabezos Altos Devonian outcrops in the Montalbán Anticline; NI, Nigüella; T, Tabuenca;). C. Location of sections having yielded the studied placoderms remains (1, Los Poyales; 2, Mariplό).
Modified from Botella et al., 2006.

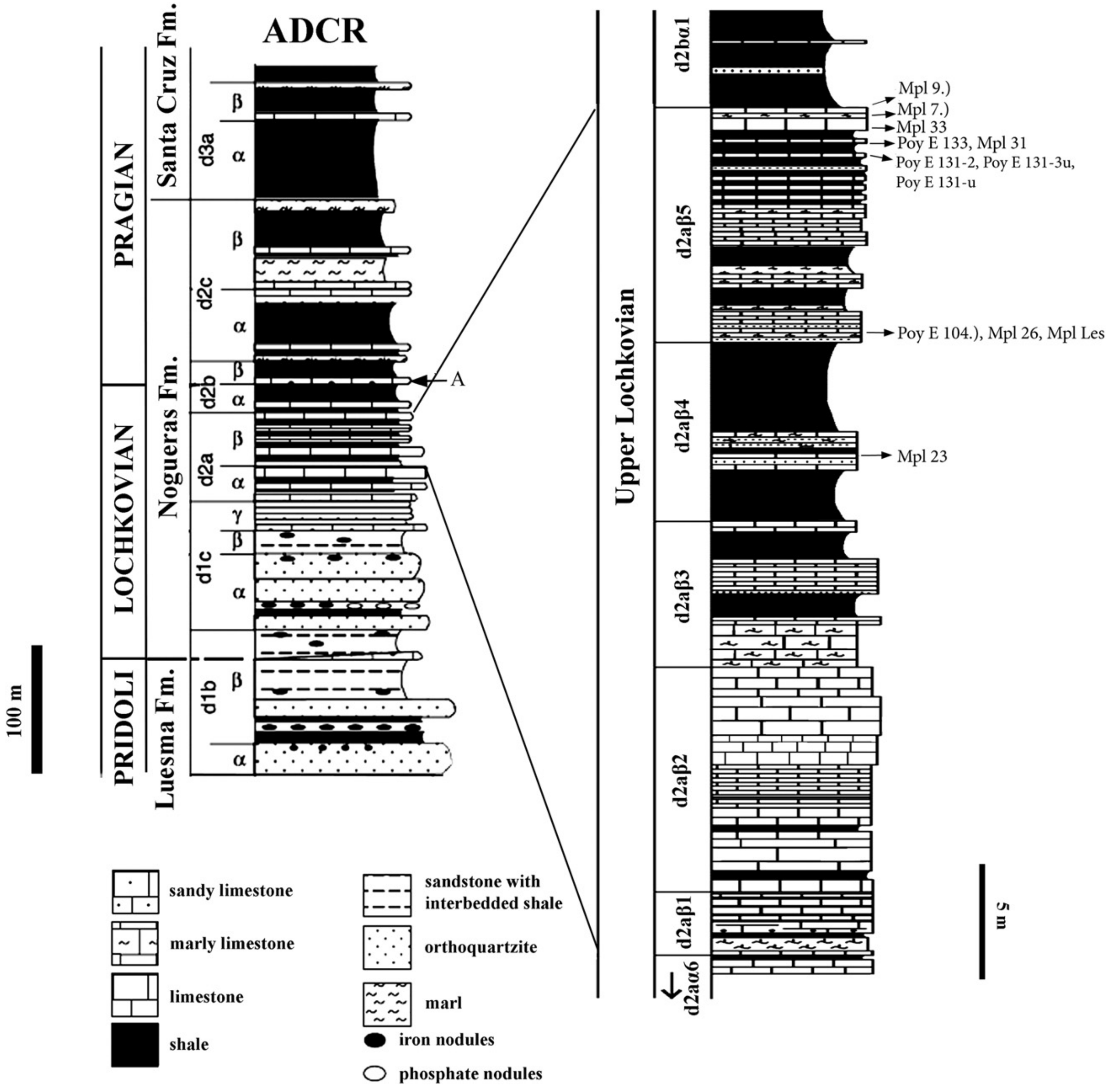

Fig. 2. Synthetic stratigraphic column of the Nogueras Formation in the ADRC (left) and detailed column of submember d2aβ (right), based mainly in section Poyales East (Dojen, 2005), with indication of levels that yielded the placoderms described in this work.
Modified from Botella et al. (2006) and Dojen (2005).

margin of this trench the unit d2aβ5 was sampled. The horizontal continuity of the litho- and biofacies in the Early Devonian strata of the ADRC allows a precise correlation between individual beds of Mariplό and Los Poyales (Wang, 1993; Dojen, 2005).

The Nogueras Formation in the ADRC (Fig. 2, left column) consists of 140 m of shallow-water marine deposits with bioclastic limestones, marls, siltstones and a few sandy lenses (palaeochannels) or more continuous thin sandy beds, which are horizontally persistent in the ADRC and correspond to "lag-deposits" (sensu Dojen, 2005). The Nogueras Formation contains the Lochkovian–Pragian boundary which is traced just below the "Leitbank A" (bed A, Fig. 2, left column). This "Leitbank A" is a laterally continuous dark mudstone bed, 35–50 cm thick, where the index brachiopod *Vandercammenina sollei* Carls, 1986 appears (indicating the beginning of the Pragian in Rhenish facies; Carls and Valenzuela Ríos, 2002). The lower 39 m of the Nogueras Formation (submembers d2aα to d2aβ) are essentially an alternation of brachiopod shelly limestones, shales and siltstones, always indicating very shallow water environments, although some transgressive–regressive tendencies can be recognised.

Placoderms occur in units d2aβ4 and d2aβ5 (Fig. 2, right column and Appendix 1). The presence of lumachel limestones with clear-water brachiopods ("*Uncinulus*" and *Howellella* (*Iberohowellella*) *hollmani*) in units d2aβ2 and d2aβ3 can indicate a transgressive tendency, although the top of submember d2aβ is characterised by a rapid shallowing (with two centimetre-thick beds full of bivalves; Carls, 1999; Dojen, 2005). Placoderm remains are particularly abundant in some beds associated with large colonies of the brachiopod C*ryptonella* in life position, at the base of the unit d2aβ5.

3. Material and methods

Placoderm remains were retrieved by splitting shelly limestones and dissolving the carbonate matrix with formic acid (5–10%). They are isolated plates and fragments of the head and trunk armour. Their preservation allows a detailed description of the external and internal morphologies (see supplementary information). Specimens were photographed with a JVC TK-1280E digital camera after being whitened with ammonium chloride sublimate. Non-placoderm remains found in the residues were kept for further studies, some of them being mentioned in this article (see Martinez-Pérez et al., 2010 for a detailed study). The placoderm material comprises a total of 53 specimens housed at the Museum of Palaeontology of the University of Zaragoza, identified by the initial MPZ followed by their related museum number (MPZ 2009/77 to MPZ 2009/125). A list of the material is given in Appendix 1.

3.1. Abbreviations

3.1.1. Anatomical terms abbreviations

AVL, anterior ventrolateral plate; cr.pd, posteromedian crest of the median dorsal plate; d.end, endolymphatic duct; IL, interolateral plate; lc, lateral sensory line groove; ld, anterior dorsolateral sensory line groove; M, marginal plate; oa.ADL, overlap area for the anterior dorsolateral plate; oa.AL, overlap area for the anterolateral plate; oa.MD, overlap area for the median dorsal plate; oa.PDL, overlap area for the posterior dorsolateral plate; oa.PL, overlap area for the posterolateral plate; oa.SO, overlap area for the suborbital plate; PaN, paranuchal plate; pect.n, pectoral notch (of the anterolateral or anterior ventrolateral plate); PM, postmarginal plate; pmc, postmarginal sensory line groove; q.ins, insertion area of the cartilaginous quadrate; s, spine or scar insertion for spine; s.AL, groove on spinal plate for insertion of the anterolateral plate; s.Sp, insertion area of spinal plate; scap, imprint of the scapulocoracoid; sorc, supraoral sensory line groove; Sp, spinal plate; and vasc, moulded vascular canals. (Abbreviations for supplementary figures are given in the on-line supplementary information.)

3.1.2. Institutional abbreviation

MPZ, Museum of Palaeontology of the University of Zaragoza (Spain).

3.2. Systematic palaeontology

An exhaustive list of the material is given in Appendix 1.

Recent and exhaustive descriptions of the Podolian forms of the arthrodire placoderms *Kujdanowiaspis podolica* and *Erikaspis zychi* are given in Dupret et al. (2007) and Dupret (2010). Recent discussion about the phylogeny of the Arthrodira, with emphasis on the Actinolepidoidei, as well as the order of appearance of the arthrodiran characters is given in Dupret et al. (2009; Figs. 3–4). Additional information on the Spanish material is provided on-line (Supplementary information). Note that the specimens from Podolia, being preserved in a clastic matrix (Old Red Sandstone facies), have been distorted somewhat by compaction. The Spanish material by contrast is undistorted.

Class Placodermi McCoy, 1848.

Order Arthrodira Woodward, 1891.

Suborder Actinolepidoidei Miles, 1973.

Family Kujdanowiaspididae Berg, 1955.

Kujdanowiaspis podolica (Brotzen, 1934).

(Fig. 3A-I and Figs. suppl. 1–2).

Occurrence—Middle part of the late Lochkovian of Celtiberia (Spain).

Description—Two specimens (MPZ 2009/98 and MPZ 2009/109, Fig. 3A–B) are parts of the skull roof, one being an isolated left paranuchal plate (specimen MPZ 2009/98, Fig. 3A), the other showing partially the left marginal, postmarginal and paranuchal plates (specimen MPZ 2009/109, respectively M, PM and PaN, Fig. 3B), together with the associated infraorbital, postmarginal and lateral sensory line grooves (respectively ioc, pmc, lc, Fig. 3B). The ventral (internal) sides of the specimens show part of the endolymphatic duct (d.end, Fig. 3A2).

The median dorsal plate (Fig. 3D–E, and Fig. suppl. 1D–F) is as wide as long and typically roof-shaped. A posteromedian crest (cr.pd, Fig. 3D) is visible on the specimens where it has not been abraded. The tubercles are smaller in the median anterior part of the plate; laterally and posteriorly to this area, they can fuse into concentric ridges.

One posterior dorsolateral plate (PDL, specimen MPZ 2009/85, Fig. 3C and Fig. suppl. 2A) shows the overlap areas for the median dorsal, the anterior dorsolateral, the anterolateral and posterolateral plates (oa.MD, oa.ADL, oa.AL, oa.PL, Fig. 3C and Fig. suppl. 2A). Its shape compares perfectly with that of the Podolian specimens of *K. podolica*.

The adult anterolateral plate (AL, Fig. 3F and Fig. suppl. 2B) is as high as long, as in the Podolian *Kujdanowiaspis podolica*. However, one small specimen shows an outline higher than long, together with rounded corners (MPZ 2009/93, Fig. 3G and Fig. suppl. 2C); this pattern is identified as a juvenile character. It is also noteworthy that on such a juvenile specimen the overlap areas represent over one half of the inner side of the plate. The tuberculation closely resembles that of the Podolian specimens of *Kujdanowiaspis podolica*.

The spinal plate (Sp, Fig. 3H–I and Fig. suppl. 2D–F) is gently curved posteromesially. Large tubercles are visible on its lateral side, sometimes merging into thick ridges. The mesial side of the spinal plate shows several anteriorly directed spinelets, as is the case in the Podolian specimens of *K. podolica* (Dupret, 2010). However, these spinelets are more numerous in the Spanish specimens than the Podolian ones; this is probably related to the size of the animal, because the spinelets themselves have approximately the same size in the Spanish and Podolian specimens.

The material includes several post-median dorsal plates (see supplementary information on-line; Fig. suppl. 2G–H) that covered the tail dorsally.

Erikaspis zychi (Stensiö, 1945) (Fig. 3J–N and Fig. suppl. 3).

Occurrence—Middle part of the late Lochkovian of Celtiberia (Spain).

Description—Like in Podolia, the material of *Erikaspis* is less abundant than that of *Kujdanowiaspis* (Dupret and Blieck, 2009: Fig. 1). No skull roof element has been found. A right postsuborbital plate has been identified (specimen MPZ 2009/104; Fig. 3J3C and Fig. suppl. 3B), the internal surface of which shows the insertion scar for the quadrate cartilage (q.ins, Fig. 3J2) and the overlap area for the suborbital plate (oa.SO, Fig. 3J2).

The median dorsal plate (Fig. 3K3C and Fig. suppl. 3C) is about as wide as long, as in all Actinolepidoidei, though flatter than its homologue in *Kujdanowiaspis podolica*. Its shape compares well with that of *E. zychi* from Podolia (Fig. suppl. 3C). It is covered with large rounded tubercles, more regularly distributed than in the Podolian specimens.

The anterolateral plate (Fig. 3L and Fig. suppl. 3D–E) is higher than long, like in *Erikaspis zychi* from Podolia (Dupret et al., 2007: Fig. 10E–F) and in *Actinolepis magna* from Estonia and Latvia (Mark-Kurik, 1973: text-Fig. 11B).

For the first time, some post-median dorsal plates (for the dermal cover of the tail; Fig. 3M and Fig. suppl. 3F) are identified for the genus *Erikaspis*. These plates, because of both their size and coarse tubercles, can only be attributed to *Erikaspis*, and not to *Kujdanowiaspis*. Some of them show a little spine or ridge (s, Fig. 3M and Fig. suppl. 3F), as is the case in the Podolian specimens of *K. podolica* (Dupret, 2010), or a scar or the insertion of the latter.

A puzzling elongated and curved element (specimen MPZ 2009/88, Fig. 3N and Fig. suppl. 3G) may be a dermal bone associated with the pelvic girdle (D. Goujet, com. pers.) as seen in the actinolepid *Sigaspis lepidophora* Goujet, 1973, from Spitsbergen. However, this is a tentative identification, both anatomically and taxonomically.

Order Acanthothoraci Stensiö, 1944.

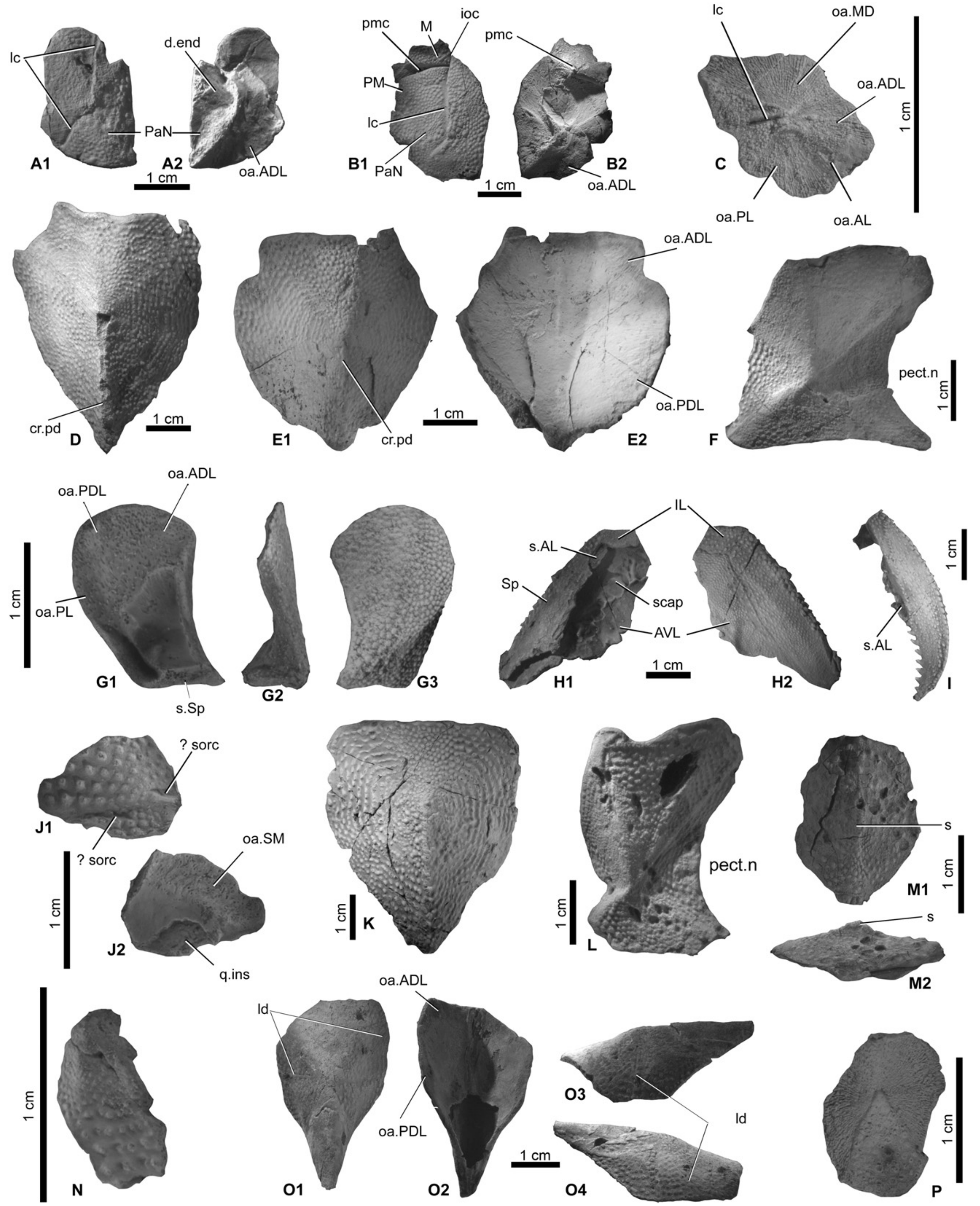

Fig. 3. Placoderm material from the Lochkovian of Spain. A–I: *Kujdanowiaspis podolica* (Brotzen, 1934). J–N: *Erikaspis zychi* (Stensiö, 1945). O: *Palaeacanthaspis* aff. *P. vasta* Brotzen, 1934. P: possible ?Ptyctodontida Gross, 1932 (external view, specimen MPZ 2009/86). *Kujdanowiaspis podolica*: A. Left paranuchal plate (specimen MPZ 2009/99) in dorsal (A1) and ventral (A2) views. B. Left paranuchal, marginal and paranuchal plates (specimen MPZ 2009/109b) in dorsal (B1) and ventral (B2) views. C. Right posterior dorsolateral plate (specimen MPZ 2009/85) in external view. D. Median dorsal plate (specimen MPZ 2009/90) in dorsal view. E. Median dorsal plate (specimen MPZ 2009/109a) in dorsal (E1) and ventral (E2) views. F. Left anterolateral plate (specimen MPZ 2009/97) in external view. G. Left anterolateral plate of a juvenile individual (specimen MPZ 2009/93) in internal (G1), anterior (G2) and external view (G3). H. Part of the left ventral armour (specimen MPZ 2009/103) in dorsal internal (H1) and ventral external (H2) views. I. Right spinal plate (specimen MPZ 2009/98) in dorsal view. *Erikaspis zychi*: J. Right postsuborbital plate (specimen MPZ 2009/104) in external (J1) and internal view (J2). K. Median dorsal plate (specimen MPZ 2009/111) in dorsal view. L. Left anterolateral plate (specimen MPZ 2009/84) in external view. M. Postmedian dorsal plate (specimen MPZ 2009/125c) in dorsal (M1) and right lateral views (M2). N. Possible pelvic girdle (specimen MPZ 2009/88). *Palaeacanthaspis vasta*: O: Incomplete median dorsal plate of *Palaeacanthaspis* aff. *P. vasta* Brotzen, 1934, in dorsal (O1), ventral (O2), left lateral (O3) and right lateral views (O4) (specimen MPZ 2009/83). Possible ?Ptyctodontida: P: Anterior median ventral plate. Scale bars equal 1 cm.

Family Palaeacanthaspididae Stensiö, 1944.

Palaeacanthaspis aff. *P. vasta* Brotzen, 1934 (Fig. 3 and Fig. suppl. 1I).

Occurrence—late Lochkovian of Celtiberia (Spain, middle part of Nogueras Fm.).

Description—One high-crested median dorsal plate (MPZ 2009/83, Fig. 3O and Fig. suppl. 4A) of the acanthothoracid *Palaeacanthaspis* is encountered in the present material. It is very similar in shape and size to the original material described by Stensiö (1944:Figs. 3, 5, pl. 2 Fig. 1, 3, pl. 3 Fig. 1) and Denison (1978: Fig. 23A). All tubercles are abraded apically, but their bases are clearly rounded. No stellate tubercle has been found on the plate (although stellate tubercles are common in the order Acanthothoraci—see Denison, 1978: p. 34, and *a fortiori* on the Podolian specimens; it is noteworthy that the acanthothoracid *Breizosteus armoricensis* from Brittanny, France, possesses rounded tubercles only; Goujet, 1980). As a consequence, we only refer this specimen to *Palaeacanthaspis* aff. *P. vasta*.

The lateral (external) side shows one pair of posterodorsally directed grooves (ld, Fig. 3O1, 3–4); these were most likely part of the sensory line system and were probably connected to the lateral line groove of the anterior dorsolateral plate.

The posterior half of the dorsal plate consists in a hollow, tapering, posteriorly oriented spine, in which vascular canals are preserved (Fig. suppl. 4A5).

Order ?Ptyctodontida Gross, 1932.

An isolated median ventral plate belongs to a possible ptyctodontid (specimen MPZ 2009/86; Fig. 3P and Fig. suppl. 4B).

4. Discussion

4.1. A brief systematic remark: what are “actinolepids”?

The vernacular term “actinolepid” has been used in the literature to refer to three distinct taxa: the grade Actinolepidoidei (a paraphyletic group at the base of the arthrodires), the grade Actinolepida (a more restricted group that excludes Antarctaspididae, Wuttagoonaspididae and Phyllolepida), and the clade Actinolepididae (*Actinolepis* + *Bollandaspis*). In this paper the term refers throughout to the grade Actinolepida. For a more detailed discussion see Supplementary Information.

4.2. Faunal links of Early Devonian vertebrates between Celtiberia and Podolia—a palaeobiogeographic scenario

Different palaeogeographic models have been proposed for the relationships of Laurussia (including Baltica), Gondwana and Gondwana-derived microcontinents (including Ibero-Armorica and Bohemia) during Ordovician to Late Carboniferous times. Most of the differences between these models concern the position and duration of wide oceans between these areas, that acted as geographical barriers against the dispersal of coastal faunas, as well as the collision time of Gondwana and/or Gondwana-derived terranes against Laurussia (see, for example, Young, 1981, 1986, 1987; Galle et al., 1995; Königshof and Schindler, 2003; Dojen, 2005; Linnemann, 2007; but see Carls, 2001, 2003; Dojen, 2005 for critical reviews). Some Early Devonian palaeogeographic reconstructions (mainly following Cocks and Fortey, 1982; Paris and Robardet, 1990; Cocks and Torsvik, 2002) show a large ocean, several thousand kilometres wide (i.e., the Rheic Ocean sensu Cocks and Fortey, 1982), between ancient Podolia (i.e., the southern margin of Baltica) and ancient Iberia (i.e., the alleged northern margin of Gondwana (Fig. 4B) or part of an independent Armorica palaeoblock (Fig. 4C)). However, other authors consider that during the early Devonian this “Rheic Ocean” was not more than a few hundred kilometres wide (e.g., Scotese, 1997; McKerrow et al., 2000). Considering that the palaeolatitudes are relatively well established for Laurussia and major parts of Gondwana for this time (Cocks and Torsvik, 2002; Torsvik and Cocks, 2004; Cocks and Torsvik, 2006), and that both Podolia and Iberia belong to an intra-tropical zone, the main problem in palaeogeographic reconstructions remains the determination of palaeolongitudes. Nevertheless, recent attempts have used

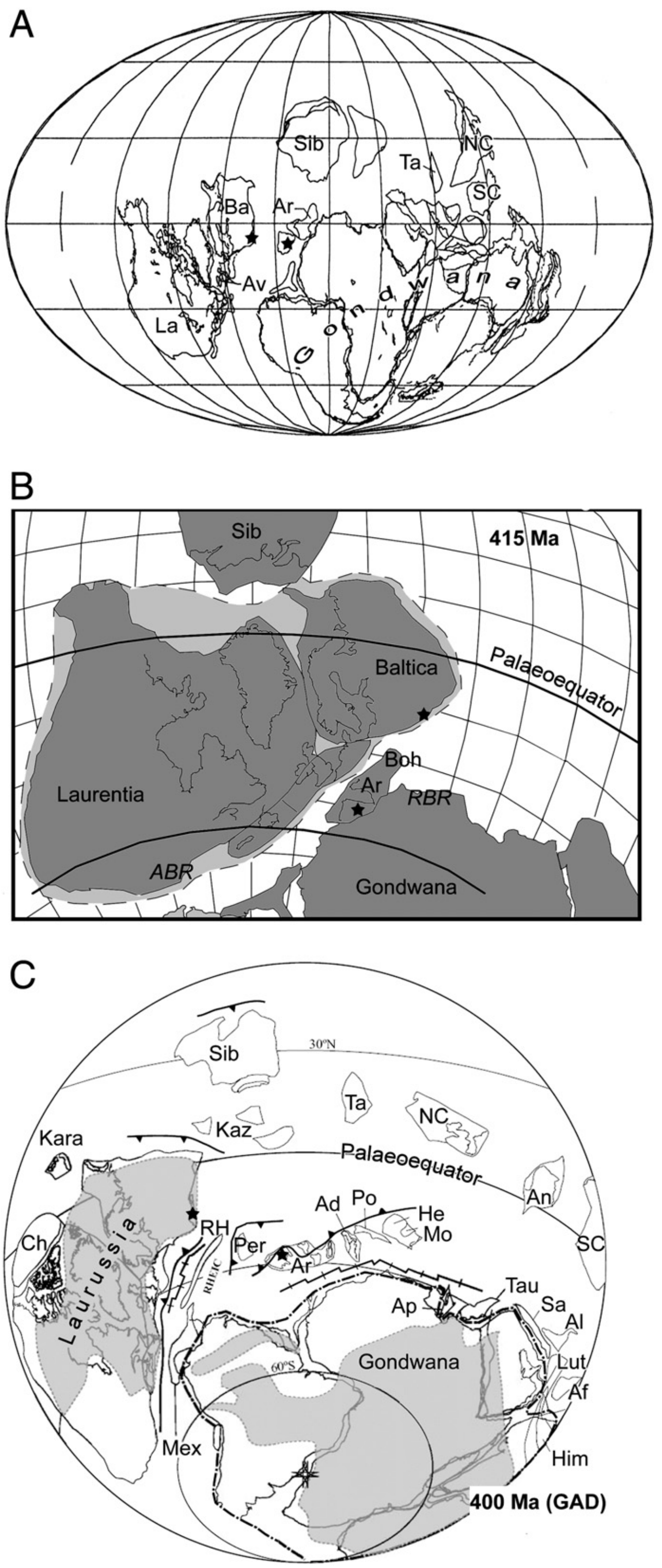

Fig. 4. Different palaeogeographic reconstruction hypotheses for the Early Devonian. The position of both ancient Podolian and Spain are indicated with black stars. (A from Li et al., 1993: Fig. 2.6; B slightly modified after McKerrow et al., 2000: Fig. 2; C from Torsvik and Cocks, 2004: Fig. 5). Key: ABR, Appalachian Brachiopod Realm; Ar, Armorica; Av, Avalonia; Ba, Baltica; Boh, Bohemia; La, Laurentia; NC, North China; RBR, Rhenish Brachiopod Realm; RH, Rheno-Hercynian Terrane; SC, South China; Sib, Siberia; and Ta, Tarim.

reconstructed Large Igneous Provinces to recover the palaeolongitudes, as far back as the Pangean assembly (c. −320 Ma) and possibly to the Late Cambrian (Torsvick et al., 2008). Fig. 4 summarises different hypotheses for the position of Laurussia vs. Gondwana during the Early Devonian.

Faunal links between Celtiberia (ADRC) and Podolia during the early Devonian that have been proposed recently by Dojen (2005) are based on neritic ostracod taxa known only from these two areas. Ostracods like *Gibba* Fuchs, 1919 and *Ponderodictya mirabilis* Abushik, 1968, evidence shallow neritic migration routes between Podolia (Baltica) and Celtiberia (Perigondwana) within the interval mid-Lochkovian to mid-Pragian.

Until now, the only vertebrate taxon known to be shared by Podolia and Celtiberia was the thelodont *Turinia pagei*, which occurs in the Lochkovian of both areas (Karatajūtė-Talimaa, 1978; Botella et al., 2006). But as this species is also widespread in the Lochkovian of many other regions (most recent review in Märss et al., 2007), it could not prove any particular link. However, the placoderm assemblage described here from the Lochkovian of Celtiberia is very similar to, and contemporaneous with, that encountered in the Lochkovian of Podolia (Ukraine). Moreover, since most of the shared taxa are – up to now – only reported from these two areas, they provide circumstantial evidence for close neritic connections between Celtiberia and Podolia.

In Celtiberia, all the known remains of both arthrodire taxa are restricted to the units d2aβ4 and d2aβ5 (Fig. 2), dated as early Late Lochkovian according to numerous faunal analyses and correlations by Carls (Carls, 1999; Dojen, 2005 and references therein). The stratigraphic occurrence of these taxa in Celtiberia is consistent with that observed from the fossil record in Podolia, where the species *Kujdanowiaspis podolica* and *Erikaspis zychi* occur in the Dnister Series (ranging from Late Lochkovian to Pragian; Dupret and Blieck, 2009).

As for the Celtiberian specimen assigned to *Palaeacanthaspis* aff. *P. vasta,* it comes from sample Mariplo 9.) (i.e., top of d2aβ5, late Lochkovian, Fig. 2) which might be slightly younger than the Podolian Chortkov stage from where *Palaeacanthaspis vasta* is reported (Middle Lochkovian; Brotzen, 1934:114; Stensiö, 1944:3).

Discoveries of other vertebrate microremains during the preparation of the placoderm material of Celtiberia, provide additional evidence of Early Devonian faunal links between Celtiberia and Podolia. The dissolution of the placoderm-bearing carbonates with formic acid yielded numerous microichthyoliths, mainly acanthodian and chondrichthyan scales. Some of the chondrichthyan scales belong to *Seretolepis elegans* Karatajūtė-Talimaa, 1968, and *Altholepis composita* Karatajūtė-Talimaa, 1997 (Martinez-Pérez et al., 2010, for a more detailed study). Previously, these taxa had been reported only from the Lochkovian of Podolia (Karatajūtė-Talimaa, 1968, 1997) and the Lochkovian of the Mackenzie Mountains (Canada) (Wilson and Hanke, 1998; Wilson et al., 2000), and as a consequence have been considered for a long time as endemic to Laurussia.

Additionally, the most abundant spiriferid brachiopod of this interval in Ibero-Armorica is *Howellella lunae* Gourvennec, 1985, which maybe a synonym of *H. salezczykiensis* (Koslowsky, 1929) in the Chortkov stage of Podolia.

In summary, the close palaeobiogeographic connections between Celtiberia and Podolia during Lochkovian–Pragian times proposed by Dojen (2005) based on ostracods are clearly supported by the data of the early vertebrates reported here. Since three placoderm species (i.e. the 'actinolepids' *Kujdanowiaspis podolica* and *Erikaspis zychi*, the acanthothoracid *Palaeacanthaspis* aff. *vasta*) are known exclusively in the Lochkovian from these two areas and since the chondrichthyans *Seretolepis elegans* and *Altholepis composita* have only been reported from one additional Laurussian locality (Canada), these vertebrates most likely characterise a particular region. The lack of this faunal association in any other areas and the general shapes of the heavily body-armoured placoderms suggest that these fishes were not able to cross large oceanic basins, though it should be noted that according to Aleyev (1977), fishes longer than 20 cm do not depend on oceanic currents. Furthermore, it is a common argument in palaeobiogeography that the shallow neritic ostracods (like those shared by Celtiberia and Podolia) lack pelagic larval stages, which delimits their migrations via deep waters, but this does not exclude migrations in coastal waters.

The present palaeontological evidence does not support the existence of a large ocean between Celtiberia (peri-Gondwanan or north-Gondwanan region) and Podolia (Laurussia) during the Early Devonian as suggested by several authors (Cocks and Fortey, 1982; Paris and Robardet, 1990; Robardet et al., 1991; Cocks and Torsvik, 2002; Torsvik and Cocks, 2004), but rather favours reconstructions showing the close proximity of Armorica and Baltica at this time (McKerrow and Scotese, 1990; McKerrow et al., 2000; Carls, 2001, 2003). These evidences are fully compatible with the model of the Variscan Mobile Crustal Field (VMCF) of El Hassani et al. (2003), that makes the constructions of the "Rhenis Ocean" unnecessary.

The detailed evaluation of the stratigraphic distribution of the vertebrate taxa shared by Podolia and Celtiberia reveals that *Palaeacanthaspis* aff. *P. vasta*, *Seretolepis elegans* and *Altholepis composita* occur in Celtiberia in the uppermost part of d2aβ, units d2aβ4 and d2aβ5 (i.e., the middle part of Late Lochkovian) whereas their first record in Podolia might be slightly older (Chortkov Stage, see above). On the other hand, the 'actinolepids' *Kujdanowiaspis podolica* and *Erikaspis zychi* occur earlier in Celtiberia (units d2aβ4 and d2aβ5, i.e. early Late Lochkovian) than in Podolia (where these species appear first in the "Old Red I zone", in the immediate vicinity of the Lochkovian–Pragian boundary; Dupret and Blieck, 2009).

According to these data, it seems that important faunal interchange between both areas occurred during the Late Lochkovian (unit d2aβ5, Fig. 2), coinciding with a rapid shallowing of the sea in Celtiberia (Carls, 1999; Dojen, 2005). Probably, faunal dispersal occurred in both directions. The occurrence of the beyrichiacean ostracod *Gibba* Fuchs, 1919 in the unit d2aβ5 of Celtiberia and its presence in the Chortkov and Ivane stages of Podolia (Dojen, 2005) support this view.

Lastly, since the Lochkovian–Pragian boundary in Podolia is indicated approximately by the first appearance of *Kujdanowiaspis buczacziensis* (Dupret and Blieck, 2009), and since no form close to this species has yet been found in the Spanish material, the vertebrate material provides further evidence for the ante-Pragian (i.e., Lochkovian) age of the fossil-bearing strata. However, it should be noted that *K. buczacziensis* is not abundant in Podolia.

The matrix composition and the associated fauna demonstrate that the Celtiberian deposits are of marine origin. In contrast, the early Devonian of Podolia has for a long time been interpreted as freshwater continental deposits, because this has been the "traditional view" of Old Red Sandstone facies. The faunal similarities suggest that the Old Red Sandstone deposits of Podolia, or at least the placoderm-bearing levels, are also of marine origin; this interpretation is further supported by the discovery of lingulid brachiopod fragments in Podolia by E. Mark-Kurik (Dupret et al., 2007:267).

5. Conclusions

For the first time, 'actinolepid' arthrodiran placoderms are reported with certainty from strata of Lochkovian age in an area related palaeobiogeographically to north-western Gondwana. The studied placoderms are identical to or very close to the contemporaneous taxa present in Podolia (Ukraine): *Kujdanowiaspis podolica*, *Erikaspis zychi* and *Palaeacanthaspis* aff. *P. vasta*.

Consequently, palaeogeographic reconstructions in which ancient Iberia and Podolia are reasonably close to each other during the Lochkovian are more probable than wider oceanic separations, which these small armoured fishes would probably have been unable to cross. This scenario is also supported by fossil chondrichthyan and ostracod evidence and fits to the model by El Hassani et al. (2003) of the Variscan Mobile Crustal Field between Baltica and north-western Gondwana in the early Devonian.

Since the invertebrate fauna (and by extension the vertebrate fauna) of Celtiberia is obviously marine, and since the Podolian and Celtiberian vertebrate faunas are almost identical, we believe that the Old Red Sandstones of Podolia (or at least the vertebrate-bearing strata) are also marine in origin, and not continental freshwater deposits.

Supplementary materials related to this article can be found online at doi:10.1016/j.palaeo.2011.07.019.

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Appendix 1. List of the material

No. of specimen	Bed	Geological sub-unit	Systematics	Anat. ID	Figured in
MPZ 2009/77	Poy E 104.)	d2aβ5	*K. podolica*	MD	Fig. suppl. 1E
MPZ 2009/78	Mpl 26	d2aβ5	*K. podolica*	Indet.	
MPZ 2009/82	Mpl 26	d2aβ5	*K. podolica*	AL?	
MPZ 2009/85	Poy E 104.)	d2aβ5	*K. podolica*	Right PDL	Fig. 3C and Fig. suppl. 2A
MPZ 2009/87	Poy E 104.)	d2aβ5	*K. podolica*	Sp	
MPZ 2009/89	Poy E 104.)	d2aβ5	*K. podolica*	2 PMD	
MPZ 2009/90	Poy E 104.)	d2aβ5	*K. podolica*	MD	Fig. 3D and Fig. suppl. 1F
MPZ 2009/91	Mpl 26	d2aβ5	*K. podolica*	MD	
MPZ 2009/92	Poy E 131-3u	d2aβ5	*K. podolica*	4 fragments	
MPZ 2009/93	Poy E 104.)	d2aβ5	*K. podolica*	left AL (juvenile)	Fig. 3G and Fig. suppl. 2C
MPZ 2009/94	Poy E 104.)	d2aβ5	*K. podolica*	Indet.	
MPZ 2009/95	Poy E 131-u	d2aβ5	*K. podolica*	MD?	
MPZ 2009/96	Poy E 133	d2aβ5	*K. podolica*	Indet.	
MPZ 2009/97	Poy E 104.)	d2aβ5	*K. podolica*	Left AL	Fig. 3F and Fig. suppl. 2B
MPZ 2009/98	Mpl 23	d2aβ4	*K. podolica*	Right Sp + scapulocoracoid imprint; incomplete	Fig. 3I and Fig. suppl. 2E
MPZ 2009/99	Poy E 104.)	d2aβ5	*K. podolica*	PaN left	Fig. 3A and Fig. suppl. 1B
MPZ 2009/100	Poy E 104.)	d2aβ5	*K. podolica*	MD	
MPZ 2009/101	Poy E 104.)	d2aβ5	*K. podolica*	Right Sp	Fig. suppl. 2F
MPZ 2009/102	Mpl 26	d2aβ6	*K. podolica*	Indet.	
MPZ 2009/103	Poy E 104.)	d2aβ5	*K. podolica*	Sp, AVL, IL	Fig. 3H and Fig. suppl. 2D
MPZ 2009/105	Mpl 23	d2aβ4	*K. podolica*	Sp, AVL	
MPZ 2009/106	Poy E 104.)	d2aβ5	*K. podolica*	PMD	Fig. suppl. 2G
MPZ 2009/107	Poy E 104.)	d2aβ5	*K. podolica*	MD + IL + AVL + AV? (left)	
MPZ 2009/108	Poy E 104.)	d2aβ5	*K. podolica*	AL (left?)	
MPZ 2009/109a	Mpl Les	d2aβ5	*K. podolica*	MD	Fig. 3E and Fig. suppl. 1D
MPZ 2009/109b	Mpl Les	d2aβ5	*K. podolica*	Left half of incomplete skull roof	Fig. 3B and Fig. suppl. 1C
MPZ 2009/110	Poy E 131-3u	d2aβ5	*K. podolica*	Sp	
MPZ 2009/112	Poy E 104.)	d2aβ5	*K. podolica*	Sp	
MPZ 2009/113	1.15 m above Mpl 7.)	d2aβ6	*K. podolica*	Indet.	
MPZ 2009/114	Mpl 26	d2aβ5	*K. podolica*	Indet.	
MPZ 2009/115	Poy E 104.)	d2aβ5	*K. podolica*	MD (fragments) + denticulated plates + 2 PMDs + fragments	
MPZ 2009/116	Poy E 104.)	d2aβ5	*K. podolica*	PMD	
MPZ 2009/117	Poy E 104.)	d2aβ5	*K. podolica*	PMD + 2 Sp	
MPZ 2009/118a	Poy E 104.)	d2aβ5	*K. podolica*	MD	Fig. suppl. 1G
MPZ 2009/118b	Poy E 104.)	d2aβ5	*K. podolica*	PMD	Fig. suppl. 2H
MPZ 2009/119	Mpl 26		*K. podolica*	MD (left half)	
MPZ 2009/120	Poy E 104.)	d2aβ5	*K. podolica*	AL right	
MPZ 2009/121	Poy E 131-2	d2aβ5	*K. podolica*	Indet.	
MPZ 2009/125a	Poy E 104.)	d2aβ5	*K. podolica*	MD	
MPZ 2009/79	Mpl Les	d2aβ5	*E. zychi*	Left AL	Fig. suppl. 3D
MPZ 2009/81	Poy E 104.)	d2aβ5	*E. zychi*	Left AL?	
MPZ 2009/84	Mpl 31-2	d2aβ5	*E. zychi*	Left AL	Fig. 3L and Fig. suppl. 3E
MPZ 2009/88	Mpl Les	d2aβ5	*E. zychi*	Pelvic girdle	Fig. 3N and Fig. suppl. 3G
MPZ 2009/104	Poy E 104.)	d2aβ5	*E. zychi*	Right PSO	Fig. 3J and Fig. suppl. 3B
MPZ 2009/111	Poy E 104.)	d2aβ5	*E. zychi*	MD	Fig. 3K and Fig. suppl. 3C
MPZ 2009/125b	Poy E 104.)	d2aβ5	*E. zychi*	PMD	
MPZ 2009/125c	Poy E 104.)	d2aβ5	*E. zychi*	PMD	Fig. 3M and Fig. suppl. 3F
MPZ 2009/83	Mpl 9.)	d2aβ5	*Palaeacanthaspis* aff. *P. vasta*	MD	Fig. 3O & Fig. suppl. 4A
MPZ 2009/86	Mpl 26	d2aβ6	?Ptyctodontida	AMV	Fig. 3P and Fig. suppl. 4B
MPZ 2009/80	Poy E 104.)	d2aβ5	placoderm indet.	Sp	
MPZ 2009/122	Mpl 26	d2aβ5	placoderm indet.	Sp?	
MPZ 2009/123	Poy E 104.)	d2aβ5	placoderm indet.	Indet.	
MPZ 2009/124	Mpl 33.)	d2aβ5	placoderm indet.	Indet.	

Supplementary on-line information on a separate file.

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