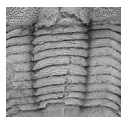


Two more Bohemian trilobites from the Ordovician of Portugal and Morocco

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Two trilobite species so far exclusive from the Dobrotivá Formation of the Prague Basin are reported for the first time outside Bohemia. The first is represented by a single specimen of *Dindymene plasi* Kielan, 1960 that occurs in Portugal within the Valongo Formation near Beloi, on the western flank of the Valongo Anticline (Central Iberian Zone). The second is *Ectillaenus benignensis* (Novák, 1918), recorded by eight articulated specimens which come from two different formations of the First Bani Group of the Moroccan eastern Anti-Atlas, located, respectively, in the upper part of the Guezzart Formation and near the top of the Ouine-Inirne Formation, both in the Jbel Bou Issidane section south of Alnif. All these occurrences are of Dobrotivian age (= late Darriwilian in the global timescale) and reinforce the palaeobiogeographical links within the north Gondwana platform. They are of special interest as it adds to a small group of species roughly coeval over a large area, and is of particular relevance for pre-Variscan palaeogeographic reconstructions. • Key words: Trilobites, Ordovician, Gondwana, palaeobiogeography, Iberia, Bohemia, Morocco.

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The faunal correspondence between Iberia and Bohemia during the Ordovician has been recognized since the times of Verneuil & Barrande (1855) and Delgado (1908), basically established through the existence of shared genera among many benthic invertebrate groups such as trilobites, echinoderms and molluscs. The evident faunal dynamics and palaeobiogeographical relationships between Iberia and Bohemia (Gutiérrez-Marco & Rábano 1987, Gutiérrez-Marco *et al.* 1999) have even allowed the adoption of a common chronostratigraphic scale (Havlíček & Marek 1973, Havlíček & Fatka 1992), with Bohemian regional stages applicable in Iberia (Gutiérrez-Marco *et al.* 1995, 2002, Sá 2003, Gutiérrez-Marco *et al.* 2008, Bergström *et al.* 2009) as well as in the Moroccan Anti-Atlas (Gutiérrez-Marco *et al.* 2003).

The faunal provincialism of the European peri-Gondwana region becomes apparent in Ordovician trilobites even at the species level, with the presence in Oretanian to Kralodvorian strata of several Bohemian taxa also recognized in Iberia. These include: *Hungioides bohemicus* (Novák, 1918), *Nobiliasaphus nobilis* (Barrande, 1846), *Parabarrandia crassa* (Barrande, 1872), *Prionocheilus mendax*

(Vaněk, 1965), *P. pulcher* (Barrande, 1846), *Selenopeltis macrophtalma* (Klouček, 1916), *S. vultuosa* Přibyl & Vaněk, 1966, *S. buchi* (Barrande, 1846), *Colpocoryphe grandis* (Šnajdr, 1956), *Zetillaenus wahlenbergianus* (Barrande, 1852) and *Symphysops armata* (Barrande, 1872); together with similar or closely related forms to *Plasiacomia rara* Hawle & Corda, 1847, *Eccoptochile clavigera* (Beyrich, 1845), *Dalmanitina* (D.) *proaeva* (Emmrich, 1839), *Stenopareia oblita* (Barrande, 1872) and *Selenopeltis kamila* Šnajdr, 1984: see Hammann (1974, 1976, 1983, 1992), Romano (1980, 1982, 1991), Rábano *et al.* (1983), Rábano (1989a–e) and Hammann & Rábano (1987). In the context of southwestern Europe, a number of Oretanian to Berounian Bohemian trilobite species have also been described from the Armorican Massif (Cavet & Pillet 1963; Henry 1980, 1989; Henry *et al.* 1997), Sardinia (Hammann & Leone 1997, 2007), and to a lesser extent from the Moroccan Anti-Atlas, where affinities occur at a generic rather than specific level (Destombes 1966, 1972), with the relative exception of the widespread genus *Selenopeltis* (Bruton 2008). In Morocco, these similarities increase significantly in the Upper Ordovician, with

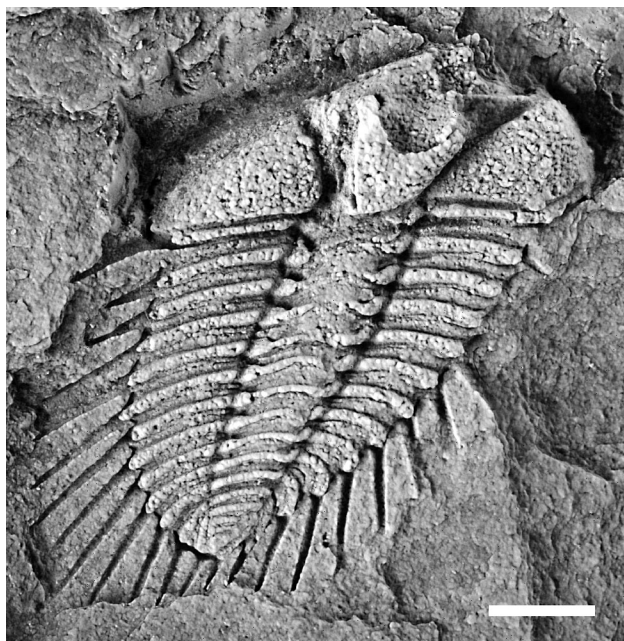


Figure 1. *Dindymene plasi* Kielan, 1960. Internal mould of a slightly deformed, articulated specimen from Beloi (northern Portugal), Valongo Formation, late early Dobrotivian (Da2) beds, top of the *Placoparia* (*Coplocoparia*) *tourneмини* Biozone. Specimen housed in the Centro de Interpretación Geológica de Canelas (Arouca, Portugal), catalogue No. CIGC-1001. Scale bar 2 mm.

the presence, among others, of *Degamella princeps princeps* (Barrande, 1872), *Selenopeltis buchi* (Barrande, 1846), *S. vultuosa* Přibyl & Vaněk, 1966, *Colpocoryphe grandis* (Šnajdr, 1956), *Prionocheilus pulcher* (Barrande, 1846), *Zdicella* cf. *zeidleri* (Barrande, 1872), *Dalmanitina* (D.) *socialis* (Barrande, 1846), *D. (D.) elfrida* Šnajdr, 1982 (= *D. proaeva* sensu Destombes, 1972), *Sokhretia* aff. *solitaria* (Barrande, 1846), *Eudolatites* aff. *dubius* (Barrande, 1846) and *Actinopeltis* aff. *grypha* (Barrande, 1852).

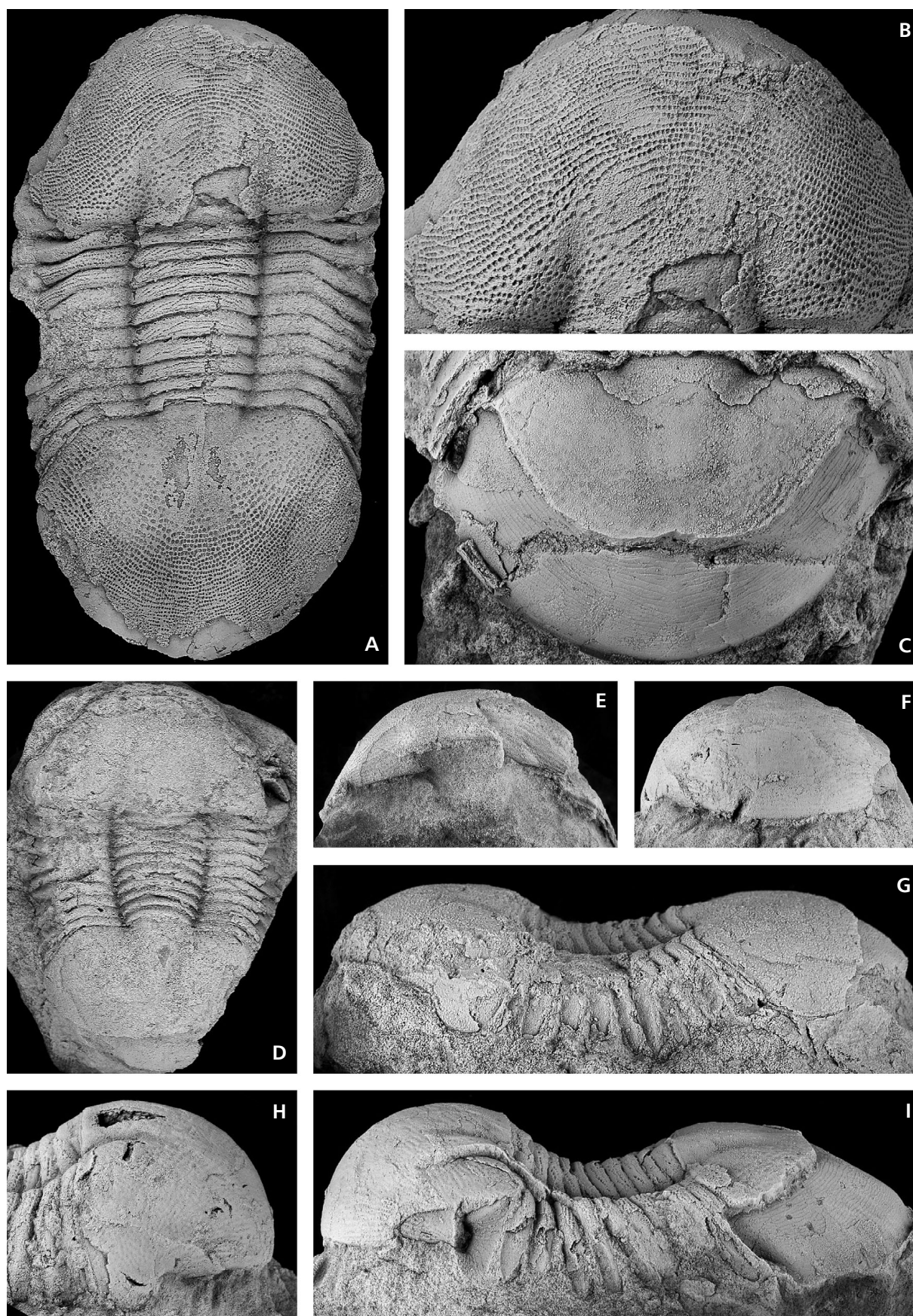
The purpose of this paper is to report the discovery of two new Bohemian trilobites in the Middle Ordovician of Portugal and Morocco, respectively, which increases, at a species level, the palaeobiogeographical links previously proposed in the literature.

Dindymene plasi from Portugal

Dindymene is a rare encrinurid trilobite, represented by about twenty European and Asian species, each restricted to one or only a few localities in the British Isles, Bohemia, Bornholm, Poland, Pamir, Kazakhstan, China and the western Appalachians (Kielan 1960, Whittard 1960, Fortey & Owens 1987, Neuman 1994, Kozák & Vaněk 1997, Qiu *et al.* 1983 and references therein). Most of their representatives come from Upper Ordovician strata, whereas the genus is rare in the Middle Ordovician, with only four taxa described from the Fennian and Aberiidian of Britain, Llandeilo of Pamir and Dobrotivian of Bohemia.

Here we report the first occurrence of *Dindymene* from the Iberian Peninsula, represented by a minute blind Bohemian species, *D. plasi* Kielan, 1960, which is recognized for the first time outside the Prague Basin. The material consists of a single articulated specimen, slightly deformed and 10 mm long, preserved as an internal mould in argillaceous shale (Fig. 1). The cephalon has a semi-circular outline, with a strongly vaulted glabella expanding forward, and with anterior corners prolonged laterally. The posterior cephalic border is straight. The fixigenae are large, with a convex genal field, ending with genal spines directed very slightly backwards. The hypostome is poorly preserved below the anterior part of the glabella. The thorax is formed by ten segments, which gradually curve backwards towards the posterior. The rachis is defined by deep dorsal furrows and gradually tapers towards the posterior part. The distal pleural portions are free and extend as thin spines, directed obliquely on the first few segments and more posteriorly in the latter ones. The pygidium is small and narrow. The rachis is wide, reaching the posterior pygidial end, and exhibits at least four distinct rings and a poorly preserved terminal part. On the pleurae there are two ribs connected with the first and second axial rings, which also extend as spines, but shorter than the thoracic ones. The dorsal surface of the internal mould shows a coarse texture, indicative of an external ornamentation with granules and pits. Librigenae and axial spines on the glabella and the fourth thoracic ring are not preserved.

Figure 2. *Ectillaenus benignensis* (Novák, 1918) from the First Bani Group, eastern Anti-Atlas, Morocco. • A – natural external mould of a flattened, complete exoskeleton in dorsal view, MGM-6334-X (× 1.35). • B – cranial region of the same specimen, showing details of the coarse ornamentation of the external surface and the smoother areas arranged in pairs, indicative of the position of glabellar and lateral muscle scars (× 2.1). • C – pygidia of complete specimen MGM-6335-X with distinct axis and exfoliated doublure (× 1.9). • D, G – internal mould of a partially complete exoskeleton in dorsal (D, × 1.3) and lateral-left views (G, × 2), specimen MGM-6338-X. • E – anterior part of the cephalon of specimen MGM-6337-X in ventral view, showing remains of the articulated rostral plate and part of the doublure of the right librigena (× 1). • F, H, I – complete specimen MGM-6336-X, with details of cephalon in frontal view showing librigenae pointing downwards (F, × 0.9), cephalon in lateral-right view with suture and rounded end of librigena (H, × 1.1), and exoskeleton in lateral-left view showing ventral doublures of pygidium and librigena (I, × 1). Specimens D and G come from locality 1826 in the upper part of the Guezzart Formation; the remaining specimens are from locality 1825, located near the top of the Ouine-Inirne Formation. Both localities lie in the Jbel Bou Issidane area south of Alnif and are of Dobrotivian (late Darriwilian) age. All material belongs to the collection of the Museo Geominero in Madrid, Spain.



The Portuguese specimen was found in the classic trilobite locality near Beloi, about 12 km east of the city of Oporto. The fossil locality was discovered by Delgado (1908) and is mentioned, among others, by Romano (1991, text-fig. 1), who provided a location map. According to this author and our own data, the trilobite horizons are located towards the upper part of the Valongo Formation (Romano & Diggins 1974), belonging to the uppermost part of the *Placoparia* (*Coplacoparia*) *tournemini* Biozone, in beds dated as latest early Dobrotivian age (= late Darriwilian on the global scale, see Gutiérrez-Marco *et al.* 2008).

Dindymene plasi Kielan, 1960 is a rare Bohemian trilobite, so far only described from a few localities in the Dobrotivá Formation (Dobrotivian) from the whole Barandian area. However, their type specimens (Kielan 1960) supposedly came from older horizons of the Šárka Formation (late Arenigian to Oretanian), but Šnajdr (1990) and Kozák & Vaněk (1997) have observed that the localities mentioned by Kielan in fact belong to the Dobrotivá Formation. The Portuguese record of this species is thus approximately of the same age as the typical Bohemian specimens, which clearly differ from the remaining *Dindymene* species in the shape of the cephalon and pygidium, and by the comparatively short, thin genal, thoracic and pygidial spines.

The occurrence of *Dindymene plasi* in the Valongo Formation adds to that of Dobrotivian cheirurids such as *Actinopeltis* (*Valongia*) *wattisoni* Curtis, 1961, *Eccoptochile* (*E.*) *almadenensis* Romano, 1980, *E. (E.?) mariana* (Verneuil & Barrande, 1855) and *E. (E.) cf. clavigera* (Beyrich, 1845), described from the Valongo Formation by Curtis (1961), Romano (1980, 1991) and Tauber *et al.* (1997). All of these taxa have early meraspid stages with a “spinose” aspect resembling adult specimens of *Dindymene plasi*, of average length 10–15 mm. However, *D. plasi* is easily recognizable by the characteristic shape of its glabella, comparatively smaller than that of the meraspid stages of the other cheirurid species, and also by its segmented pygidial rachis. Spinosity is also very different in the mentioned cheirurids (see for instance, Rábano 1989c, pl. 28, fig. 7 for *Eccoptochile*).

Ectillaenus benignensis from Morocco

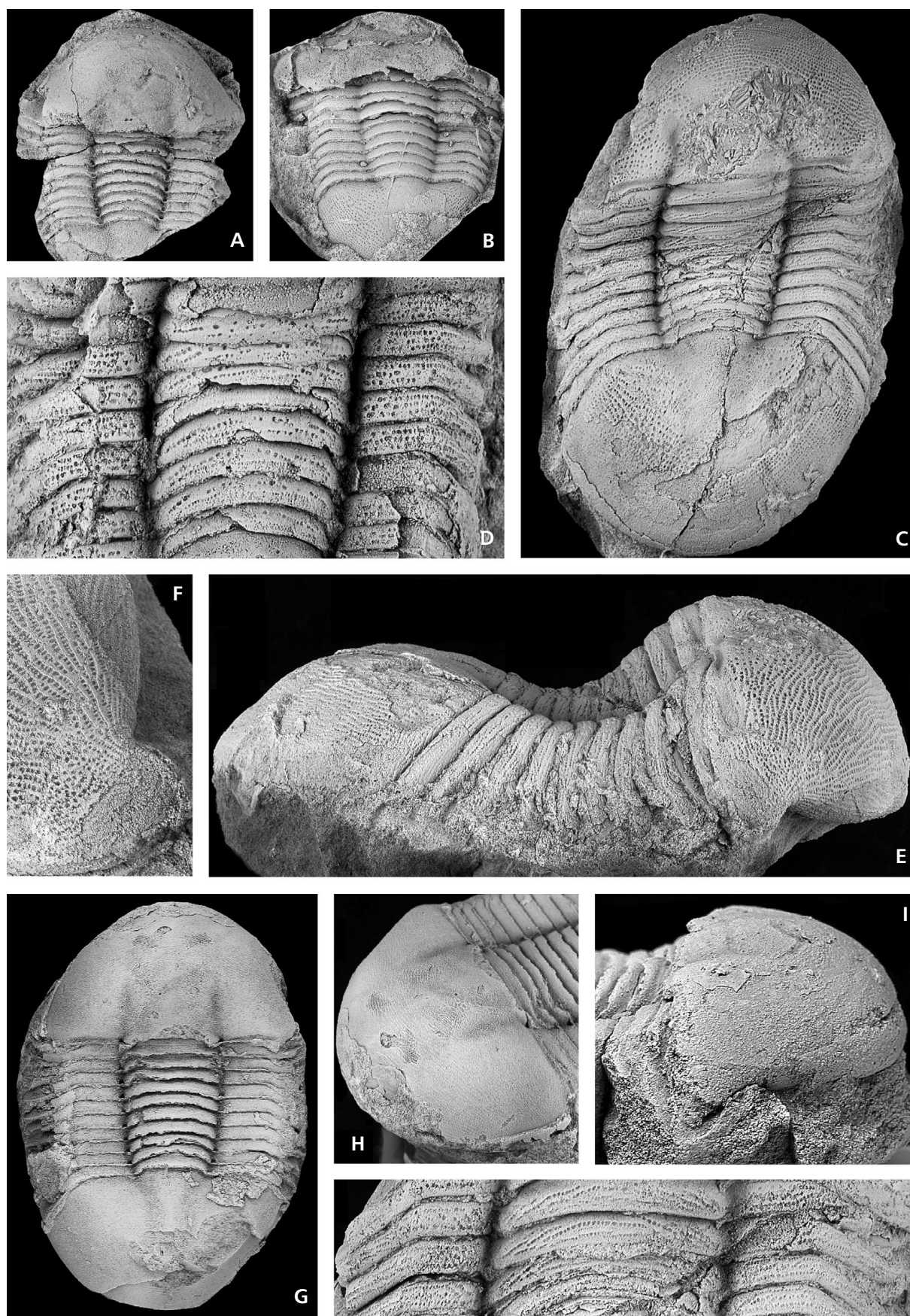
Ectillaenus is the most common illaenid trilobite occurring in the European peri-Gondwanan realm. It is known from eleven species, mainly described from Britain (Whittard 1961, Fortey & Owens 1987), Ibero-Armorica (Rábano & Gutiérrez-Marco 1983, Rábano 1989e), Germany (Budil *et al.* 2009) and Bohemia (Šnajdr 1957, Bruthansová 2003). Outside Europe, the genus has only been reported from Morocco (Termier & Termier 1950, Destombes *et al.* 1985), but so far all the specimens were listed as *Ectillaenus* sp. with the exception of a specimen from the western High Atlas and being related to *E. perovalis* (Murchison, 1839) (Termier & Termier 1950, pl. 193, figs 15–17). Doubtful records of *Ectillaenus* have also been listed from China (Zhou & Zhen 2008) and Kirghizistan (Petrunina *in* Repina *et al.* 1975).

The general biostratigraphical review by Gutiérrez-Marco *et al.* (2003) of the Middle Ordovician formations of the Moroccan Anti-Atlas produced new material in the localities numbered as 1825 and 1826 by Destombes (1985), also including some echinoderms (Chauvel 1978) and molluscs (Babin & Destombes 1990). Among the trilobites we could identify several specimens of *Ectillaenus benignensis* (Novák, 1918), which represent the first record of this species outside Bohemia.

The Moroccan *E. benignensis* material consists of eight articulated specimens, four of them exceptionally well preserved as natural external moulds in calcareous siltstone, one as a concave internal mould and three internal moulds (Figs 2, 3). The main specific characters are easily recognizable: a coarse ornamentation of large pits arranged mostly in rows which cover almost the complete dorsal surface of the vaulted carapace, but is attenuated in the pygidial rachis and in the cephalic muscle fields; semi-circular cephalon lacking eyes; librigenae narrow and with a prominent rounded end pointing downwards; pygidium moderately parabolic in outline, with axis occasionally distinct in some internal moulds, reaching 40% of the pygidial length; pygidial doublure extending for almost half of the pygidial length (sag.).

Ectillaenus benignensis is the most coarsely ornamented species of the genus (Novák 1918, Šnajdr 1984, Bruthansová 2003). In this aspect, it resembles only

Figure 3. *Ectillaenus benignensis* (Novák, 1918) from the First Bani Group, eastern Anti-Atlas, Morocco. • A, I – internal mould of a partially complete exoskeleton, MGM-6340-X, in dorsal view (A, $\times 1.3$) and detail of the cephalon, suture and librigena in lateral-right view (I, $\times 2.66$). • B – latex cast from the external mould, dorsal view, MGM-6341-X ($\times 1.3$). • C, E, F, J – natural external mould of the complete specimen MGM-6337-X in dorsal (C, $\times 1$) and lateral-right views (E, $\times 1.26$), with details of the cephalic suture and strong ornamentation of the right librigena in oblique-lateral view (F, $\times 2.3$) and the second to fourth thoracic segments (J, $\times 2$). • D – details of the external ornamentation of the last eight thoracic segments of the specimen MGM-6336-X ($\times 1.8$), see also Fig. 2F, H, I. • G, H – internal mould of a partially complete exoskeleton, MGM-6339-X, in dorsal view showing doublures on the thoracic pleurae (G, $\times 1.1$), and detail of the cephalon with muscle scars and suture, in oblique anterolateral view (H, $\times 1.46$). Specimens C–F and J come from locality 1825 near the top of the Ouine-Inirne Formation; remaining specimens are from locality 1826 in the upper part of the Guezart Formation. Both localities lie in the Jbel Bou Issidane area south of Alnif, and are of Dobrotivian (late Darriwilian) age. All material belongs to the collection of the Museo Geominero in Madrid, Spain.



E. "hughesii" (Hicks, 1875) [= *E. perovalis* (Murchison, 1839)], and both taxa were considered synonyms by Whittard (1940, 1961) and Pek & Vaněk (1989). However, Šnajdr (1957) convincingly demonstrated the differences between the British and Bohemian forms, and *E. benignensis* was recognized as a separate species also by Rábano & Gutiérrez-Marco (1983), Fortey & Owens (1987), Bruthansová (2003), Budil (1999) and Vaněk & Valíček (2001).

From a biostratigraphical point of view, *E. benignensis* is recognized from the whole Barrandian area within the Dobrotivá Formation (Dobrotivian, essentially upper Darriwilian). The Moroccan record is also Dobrotivian in age, and includes two different formations in the First Bani Group of the eastern Anti-Atlas. The specimens MGM-6338-X to MGM-6341-X (Figs 2D, G, 3A, B, G-I), come from the Destombes' locality 1826, located towards the upper part of the Guezzart Formation in the Jbel Bou Issidane area south of Alnif (geological map of Morocco, sheet Alnif to 1 : 100,000 scale, Lambert coordinates x = 521.5; y = 45.8). The specimens occur in fine calcareous sandstones associated with other trilobites (*Selenopeltis* sp., *Placoparia* (*Coplocoparia*) sp.), as well as with some diploporite echinoderms (*Calix*, *Phlyctocystis* and *Isidolocystis*). This locality, previously assigned to the Taddrist Formation by Chauvel (1978), was reviewed by Gutiérrez-Marco *et al.* (2003) and reassigned to the Guezzart Formation in beds of late early Dobrotivian age. The second fossiliferous locality provided another four specimens of *E. benignensis*, even better preserved, from calcareous and ferruginous sandstone. These were numbered MGM-6334-X to MGM-6337-X (Figs 2A-C, E, F, H-I, 3C-F, J). It corresponds to locality 1825, which lies very close to the former locality (geological map of Morocco, sheet Alnif to 1 : 100,000 scale, Lambert coordinates x = 523.3; y = 45.8), but in higher beds, occurring near the top of the Ouine-Inirne Formation. Apart from *Ectillaenus*, several other trilobite genera occur in the association (*Selenopeltis* sp., *Eccoptochile* sp., *Placoparia* sp.), as well as some molluscs (Babin & Destombes 1990). According to Gutiérrez-Marco *et al.* (2003), the locality has a late Dobrotivian age, but still within the latest Darriwilian.

Palaeobiogeographical relationships

The discovery of *Dindymene plasi* Kielan, 1960 in the Ordovician of Portugal is of prime importance because it increases the group of such Dobrotivian Ibero-Bohemian species which are roughly coeval in both areas and whose appearance is not related to the global mid Darriwilian transgression. In addition to the present form, the group also includes the benthic trilobites *Placoparia* (*Coplocoparia*) *borni* Hammann, 1971 [= *P. (C.) antiopa* Moravec,

1990 according to Havlíček & Vanek 1996] and *Eccoptochile mariana* Verneuil & Barrande, 1855 [= *E. vipera* Moravec, 1986 according to Havlíček & Vanek 1996 and Vanek & Valíček 2001], both recorded from the late Dobrotivian; the nektobenthic *Parabarrandia crassa* (Barrande, 1872), sporadically represented in some late early Dobrotivian localities of Ibero-Armorica; the diploporid *Calix purkynei* (Klouček, 1917), which occurs in the earliest Dobrotivian of Spain and at a single Bohemian locality, and the cephalopod *Trocholites fugax* (Babin & Gutiérrez-Marco, 1992). The latter is linked to a common episode of climatic disturbance in northern Gondwana (Babin & Gutiérrez-Marco 1992, Manda 2008). Similarly, the discovery of *Ectillaenus benignensis* (Novák, 1918) in the Dobrotivian of Morocco represents the first fully benthic trilobite apparently coeval in North Africa and Bohemia during the late Darriwilian, apart from some of the nektobenthic species of *Selenopeltis* reported by Bruton (2008).

According to Gutiérrez-Marco *et al.* (1999), the first generic, and even specific, similarity between Ibero-Armorican and Bohemian faunas starts by the end of the Arenigian, influenced by the global mid Darriwilian transgression. This is exemplified among the Oretanian faunas by the common occurrence of *Placoparia* (*P.*) *cambriensis* Hicks, 1875 (= *Placoparia barrandeii* Prantl & Šnajdr, 1957), *Hungioides bohemicus* (Novák, 1918), *Selenopeltis macrophtalma* (Klouček, 1916), *Babinka prima* Barrande, 1881, *Redonia deshayesi* Rouault, 1851 (= *R. bohémica* Barrande, 1881), *Coxiconchia britannica* (Rouault, 1851) [= *C. b. holubi* Kříž, 1995], *Lagynocystis pyramidalis* Barrande, 1887, *Palaeura neglecta* Schuchert, 1915, among others; or by the trilobite genera *Asaphellus*, *Nobiliasaphus*, *Bathycheilus*, *Colpocoryphe*, *Ectillaenus*, *Dionide*, *Geragnostus*, *Toletanaspis* or *Uralichas*. Some of these faunas were previously recorded in the Arenigian of Eastern Avalonia, SW France, as well as in the North African and South American margins of Gondwana (Gutiérrez-Marco & Rábano 1987, Gutiérrez-Marco *et al.* 1999). However, after the end of the influx of this global transgression, the Dobrotivian faunas abruptly decrease in similarity, with the only exceptions being the coeval taxa listed above, to which *D. plasi* in SW Europe and *E. benignensis* in N Africa are now added.

The chronostratigraphic refinement achieved in the Mediterranean regional scheme for the Middle and Upper Ordovician, allowed the recognition of a considerable diachronism in the appearance of another set of benthic to epiplanktic taxa in common between Iberia and Bohemia. The pattern was recognized among taxa recorded from the Iberian Oretanian, whose first appearance in Bohemia took place in the Dobrotivian (such as the brachiopod *Brandysia benigna* Havlíček, 1975), or those Oretanian or Dobrotivian Iberian taxa with delayed presence in Bohemia until

the Berounian or Kralodvorian. These include the trilobites *Colpocoryphe grandis* (Šnajdr, 1956) and *Nobiliasaphus nobilis* (Barrande, 1846) s.l., the ostracod *Quadritia* (*Krutatia*) *tromelini* Vannier & Schallreuter, 1983, the molluscs *Myoplusia bilunata perdentata* (Barrande, 1881) and *Technophorus sharpei* (Barrande in Perner, 1903), the echinoderms *Aristocystites metroi* Parsley & Prokop in Parsley, 1990, *A. bohemicus* Barrande, 1887, *Codiacystis moneta* (Barrande, 1887) s.l. and *C. aff. bohémica* (Barrande, 1887), the hyoliths *Leolites*, *Andalucilites* and *Recilites* and the brachiopod genera *Jezercia* and *Aegiromena*, among others. The existence of the above-mentioned taxa, appearing earlier in Iberia than in Bohemia, led Gutiérrez-Marco et al. (1999) to propose the existence of an apparent one-way migration route already established by the Middle Ordovician running eastwards from Ibero-Armorica to Bohemia.

Concluding remarks

The classic biogeographical relationships between Bohemia with Ibero-Armorica and Morocco have long been interpreted as a result of free faunal exchange, which could have operated simultaneously in all directions within the North African and European peri-Gondwana environment. This would imply an established geographic continuity, with faunal differences explained in terms of bathymetric facies, which, for instance, would have prevented the dispersal of the inshore *Neseuretus* Fauna into the deeper Bohemian environments dominated by atheloptic communities during the Middle Ordovician. However, the paleogeography of the peri-Gondwanan areas of Europe and North Africa was more complex than previously understood, and refutes a direct continuity between Iberia and Bohemia before being obscured and overwritten by Variscan tectonics. The more recent and conflicting paleogeographical models (Robardet 2003, Carls 2003, Cocks & Torvik 2006, Nance & Linnemann 2008, von Raumer & Stampfli 2008) need to be checked against the paleontological record and, in this context, the new Bohemian trilobites shared with Portugal and Morocco should be taken into account in any future and more precise palaeobiogeographical reconstruction.

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