A Kralodvorian (upper Katian, Upper Ordovician) benthic association from the Ferradosa Formation (Central Portugal) and its significance for the redefinition and subdivision of the Kralodvorian Stage

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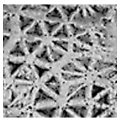

A new upper Katian (Kralodvorian Regional Stage) benthic association from the Riba de Cima Member of the Ferradosa Formation, Portugal, is described. It is dominated by bryozoans and echinoderms but brachiopods and trilobites are also present. More than 20 species of brachiopods, nine of trilobites and eight of echinoderms have been identified in the four studied localities. Among the brachiopods *Kjaerina (Villasina) meloui* Colmenar, 2016, *Dolerorthis abeirensis* Mélou, 1990 and *Bicuspina* cf. *armoricana* Mélou, 1990 are significant. These species were previously recorded only in the uppermost Rosan Formation (Armorican Massif, France). *Porambonites dreyfussi* Havlíček, 1981 is also reported in this paper for the first time besides its type horizon in the upper part of the Kralodvorian Gabian Formation (Montagne Noire, France). Most of the identified trilobite taxa were previously documented only in the Kralodvorian Cystoid Limestone Formation (Iberian Chains, Spain), except *Parillaenus*? cf. *creber* Hammann, 1992 and *Amphoriops* cf. *inflatus* (Hammann, 1992), whose referred species are also present in the upper Berounian–Kralodvorian Portixeddu Formation in Sardinia. The record of "*Ceraurinus*" *meridianus* (Hammann, 1992), "*Bumastus*" aff. *commodus* Apollonov, 1980 and *Amphoriops* cf. *inflatus* represent the first occurrence of these genera-groups in Portugal. These records are important additions to the knowledge of the Portuguese Late Ordovician benthic marine communities, providing crucial new data to constrain the biostratigraphy of the Riba de Cima Member and the palaeogeographical setting of this region at that time. In addition, some of the brachiopod occurrences with more restricted stratigraphical ranges provide invaluable tools for enabling more precise subdivision of the Kralodvorian regional stage. • Key words: South Gondwana, Riba de Cima Member, Buçaco Syncline, upper Katian, *Nicolella* Fauna.

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The *Nicolella* Fauna (Pickerill & Brenchley 1979) was the commonest brachiopod-dominated assemblage throughout high-latitude peri-Gondwana shelves during the Late Ordovician episode of global warming, the Boda Event (Fortey & Cocks 2005). This community is widely documented in the upper Katian (Kralodvorian Regional Stage) rocks of the Mediterranean region, from Spain, France and Sardinia (Colmenar 2015 and references therein). Many

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diagnostic brachiopod taxa of the *Nicolella* Fauna originated in Avalonia, Baltica and Laurentia (Williams 1963, Pickerill & Brenchley 1979, Harper *et al.* 2013), located in lower latitudes than High-Latitude peri-Gondwana during the Ordovician. As a consequence of rising temperatures during the Boda Event, carbonate sedimentation encroached High-Latitude peri-Gondwana and these taxa expanded their geographical distribution into this province, replacing endemic taxa (Villas 1985, Villas *et al.* 2002b, Boucot *et al.* 2003, Colmenar *et al.* 2013, Harper *et al.* 2013, Colmenar 2015) that then became rare or absent in the assemblages, or were displaced to higher latitudes (*e.g.* Morocco; Colmenar & Álvaro 2015).

In Portugal, diagnostic brachiopods of the *Nicolella* Community are known from the Porto de Santa Anna and Ferradosa formations (Young 1988) of the Central Iberian Zone of the Buçaco-Penacova region, Central Portugal (Young 1985, Sá *et al.* 2011, Colmenar 2015). These occurrences were first documented by Delgado (1870, 1897, 1908), who discovered fossils in these rocks for the first time and provided the earliest lists of fossils from the levels currently included in both formations. The material studied by Delgado was later revised by Young (1985), who established the current accepted lithostratigraphic scheme for the Upper Ordovician of Central Portugal (Young 1988) adding several new outcrops and reporting new fossil occurrences.

The present study reports an exceptional fossil association from the silicified limestones of the upper member of the Ferradosa Formation, the Riba de Cima Member (Young 1988), cropping out in the Penacova-Vila Nova de Poiares region (Fig. 1). The fossiliferous beds yield, in decreasing order of abundance, bryozoans, echinoderms, algae, brachiopods, trilobites and gastropods. Careful sampling during several field campaigns, together with the study of the classical Delgado's fossil collections from these beds housed in the Museu Geológico (LNEG, Lisbon), revealed the presence of previously unrecorded brachiopod and trilobite taxa in Portugal. The biostratigraphical and palaeobiogeographical significance of the new data, especially the brachiopod and trilobite taxa, are discussed. A proposal to subdivide the Kralodvorian Regional Stage is here proposed, together with a reassessment of the Kralodvorian Regional Stage itself and its boundaries.

Geographical and geological setting

The studied material comes from three localities of the Riba de Cima Member of the Ferradosa Formation, located in Sazes do Lorvão (Locality 1: 40° 18´ 25˝ N, 8° 19´ 53˝ W) and Ferradosa (Locality 2: 40° 15´ 41˝ N, 8° 14´ 53˝ W) localities of Penacova municipality and in Alveite Grande (Locality 3: 40° 13´ 11˝ N, 8° 12´ 38˝ W) locality of Vila Nova de Poiares municipality, both located in the northern part of the Coimbra district (Fig. 1).

The Ordovician rocks of the Buçaco Syncline crop out in the Penacova-Vila Nova de Poiares region, which lies in the western portion of the Central Iberian Zone (CIZ). This syncline comprises two lithostratigraphic sequences separated by an angular unconformity – the Beiras Group, a monotonous, kilometre-thick series of intercalated shales and greywackes Neoproterozoic in age; and the post-Cambrian Palaeozoic metasedimentary sequence, ranging from Lower Ordovician to the Silurian (Oliveira *et al.* 1992).

The Ferradosa Formation (> 100 m thick) was defined by Young (1985, 1988) in the Penacova region (Central Portugal) and has been assigned to the upper Berounian–Kralodvorian (*ca.* middle to upper Katian; Ka2–Ka4 stage slices of the global scale). It crops out in the southern part of the Buçaco Syncline (Penacova to Vila Nova de Poiares sectors). In the type area (near Ferradosa Village) this unit shows a faulted contact with the underlying middle to upper Berounian Louredo Formation (*ca.* upper Sandbian–middle Katian; Sa2–Ka2 stage slices), but in other sections the Ferradosa Formation exhibits a basal erosive contact, marked by a thin oolitic ironstone layer. This horizon correlates with the oolitic ironstone at the base of the Porto de Santa Anna Formation, in the northernmost part of the Buçaco Syncline.

The Ferradosa Formation comprises two members (from the base to the top): the Poiares Member, composed of decalcified marls (6–10 m thick), and the Riba de Cima Member (up to 100 m thick), comprising dolomites that are locally silicified.

The Riba de Cima Member is highly fossiliferous, except where the effects of the dolomitization and/or metamorphic processes were more intense that prevented the preservation of the fossils. Its fossil assemblages have been known for more than one hundred years (Delgado 1908) and they were previously partially studied by Young (1985; brachiopods) and Jacinto *et al.* (2015; echinoderms).

The fossils from Locality 1 (Cabeço Pedrogão – Sazes do Lorvão, Penacova) (Fig. 2A) are from the lower half of the Riba de Cima Member section in this area (Fig. 3). This locality was discovered in 1897. Young (1985, pp. 87–88) included these beds in his "well-bedded rottenstones" facies. The rocks are highly silicified, but their structure suggests that they were originally carbonates. The petrographic study conducted by Souza-Brandão (1910) identified the presence of cryptocrystalline and other forms of silica (opal), sericite, and kaolinite, although there is still some carbonate preserved. The Riba de Cima Member in this section grades up into a massive, cavernous silicified unit, possibly a silicified equivalent of the massive

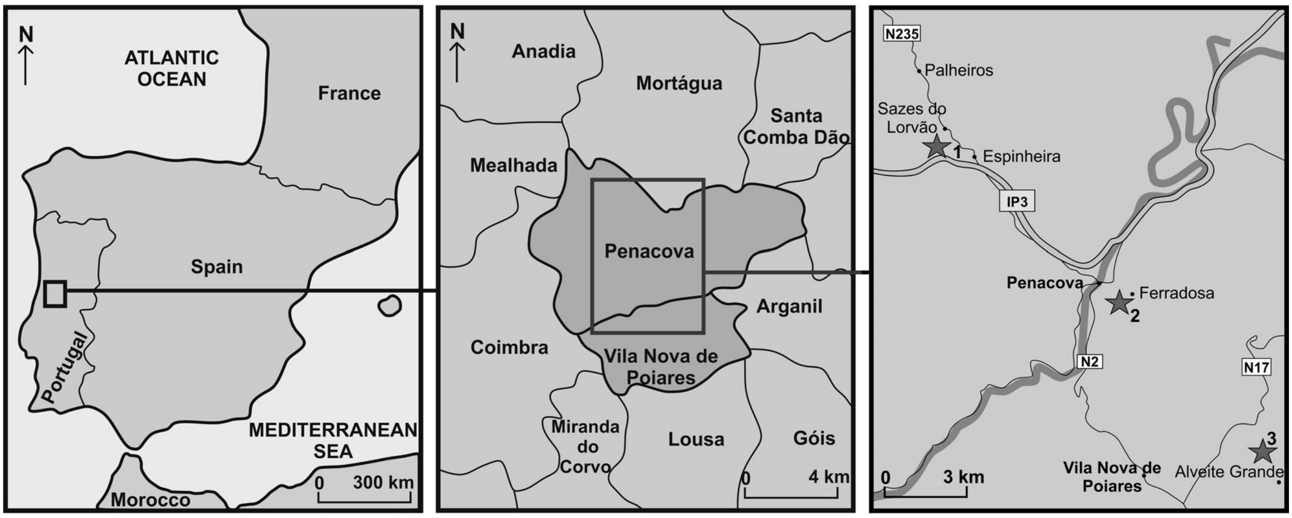


Figure 1. Geographic location of the Riba de Cima Member fossil localities. 1 – Cabeço Pedrogão – Sazes do Lorvão (Penacova); 2 – Ferradosa (Penacova); 3 – Alveite Grande (Vila Nova de Poiares).

dolomites that are exposed approximately 1.2 km to the northwest, as well as further southeast in the Buçaco Syncline.

The fossils from Locality 2 (Ferradosa, Penacova) came from a roadside outcrop of a highly faulted succession of thinly-bedded silicified rocks (Fig. 2B), probably lying stratigraphically above the massive dolomites (Fig. 3). They are faulted against Silurian mudstones to the west and their relationship to the dolomites to the east is obscured. The locality displays the youngest rocks of the Ordovician succession on the eastern limb of the syncline that are preserved in this part of the area.

The outcrop of the Locality 3 (Alveite Grande, Vila Nova de Poiares) is composed of *in situ* rock blocks and boulders (Fig. 2C). The lithology is similar to Locality 1, but the rocks are less silicified and their argillaceous component is higher. This locality is interpreted as lying approximately in the middle of the Riba de Cima Member on the eastern limb of the syncline (Fig. 3), but exposure is poor between this locality and the former dolomite quarries 400 m northwest.

Biostratigraphical and palaeobiogeografical significance of the Riba de Cima Member association

Most of the taxa recorded in the Riba de Cima Member of the Ferradosa Formation are typical of the *Nicolella* Fauna. These taxa are considered to have originated in low latitudes and to subsequently expand their geographical distribution to higher latitudes during the mid to late Katian (Ka2–Ka4 stage slices; regional late Berounian–Kralodvorian stages) Boda Event (Fortey & Cocks 2005). This expansion of the *Nicolella* Fauna is thought to have wiped-out most of the high-latitude peri-Gondwana endemic taxa (Colmenar *et al*. 2013). As a result, the brachiopod diversity in the peri-Gondwanan shelves increased considerably, with decreasing endemicity (Colmenar 2015). In this context, the biostratigraphical and palaeobiogeographical significance of relevant brachiopod (Figs 4, 6, 7) and trilobite (Figs 5, 7) taxa identified in the Riba de Cima Member association are discussed below. The echinoderm (Figs 5, 7) taxa present in the studied association, despite not having been the subject of a thorough study, are in agreement with records of coeval echinoderm faunas in Spain and Sardinia (Gutiérrez-Marco *et al.* 1996b; Zamora *et al.* 2014a, b).

Brachiopods. – The brachiopod genus *Nicolella* Reed, 1917 is widely represented in Avalonian records throughout the Katian stage (Cheneyan to Rawtheyan regional stages), represented by the species *Nicolella actoniae actoniae* (J. de C. Sowerby, 1839)*, N. actoniae multicostata* Harper, 1984*, N. actoniae obesa* Williams, 1963, *N. actoniae ramosa* Harper, 1984 and *N. asteroidea* Reed, 1917. The *Nicolella* genus was also documented in Baltica [Estonia (Vinn 2005), Lithuania (Paškevičius 1994), Norway (Harper *et al*. 1984)]; Midland Valley terrane [Girvan, Scotland (Williams 1962)]; and Sibumasu, Burma (Cocks & Zhan 1998)]. In the High-Latitude peri-Gondwanan region only the species *N. decemcostata* Havlíček 1981 from the middle to upper Katian (upper Berounian to Kralodvorian regional stages) Gabian Formation of the Montagne Noire has been defined. The remaining peri-Gondwanan material has been assigned to the Avalonian species (*e.g.* Havlíček 1981, Villas 1985, Mélou 1990, Sayar & Cocks 2013). However, its specific assignment is unclear, since several authors recognize important in key diagnostic characters such as the interarea attitude (Villas 1985, Mélou 1990), the number of ribs or the growth stage in which the ribs start branching (Colmenar unpublished data) in specimens of the same fossil assemblage. Thus, a comprehensive taxonomic revision focused on these key characters needs to be undertaken in the future, in order to properly classify the Portuguese specimens documented here and the remaining peri-Gondwanan material.

The oldest representatives of *Porambonites* Pander, 1830 are known from Baltica, namely *P. intermedius* Pander, 1830 from the Floian (Billingen Regional Stage) of Estonia and north-west European Russia and *P. trigonus* Pander, 1830 (= *P. subrecta* Pander, 1830; *P. latissima* Pander, 1830; *P. parva* Pander, 1830) from the Dapingian–lower Darriwilian (Volkhovian Regional Stage) of north-west European Russia. Thus, *Porambonites* is considered to have originated in Baltica. In the High-Latitude peri-Gondwana realm three *Porambonites* species have been described: *P. havliceki* Mergl, 2013 from the upper Arenigian (lower Darriwilian) Šárka Formation of the Czech Republic; *P. magnus* (Meneghini, 1880) from the middle part of the Kralodvorian Portixeddu Formation of Sardinia and *P. dreyfussi* Havlíček, 1981 from the upper part of the Kralodvorian Gabian Formation of the Montagne Noire. Also, specimens assigned tentatively to this genus are known in High-Latitude peri-Gondwana probably since the upper Dapingian [*Porambonites*? sp. from the Klabava Formation, Barrandian area (Mergl 2013)]. *P. magnus* and *P. dreyfussi* are frequent in peri-Gondwanan Kralodvorian assemblages, especially in Portugal, Spain, France and Sardinia. In the Riba de Cima Member, *P. dreyfussi* is consistently present in stratigraphically higher levels than the species *P. magnus*. This species succession will be discussed in the following section.

The genus *Eoanastrophia* Nikiforova & Sapelnikov, 1973 is known from the lower Sandbian–upper Katian of Altai (Kulkov & Severgina 1989), the Sandbian–Katian of the Zeravshan Range, Tadzhikistan and from the lower Katian of the Chingiz Terrane (Klenina *et al.* 1984) and New South Wales (Percival 2009). In High-Latitude peri-Gondwana, this genus is only represented by the species *E. pentamera* (Meneghini, 1857), reported from the Kralodvorian of the Armorican Massif (Mélou 1990), Montagne Noire (Havlíček 1981), Bohemia (Havlíček & Mergl 1982, Štorch & Mergl 1989, Mergl 2011b), Carnic Alps, Sardinia (Havlíček *et al.* 1987, Leone *et al.* 1991), Spain (Villas 1985, Gutiérrez-Marco *et al.* 1996a) and Portugal (Colmenar 2015, this paper).

Saukrodictya Wright, 1964 species are documented from the Upper Ordovician to lower Silurian rocks of Avalonia, Baltica, Siberia and High-Latitude peri-Gondwana. Two species have been described from the peri-Gondwanan fossil record: *S. porosa* (Havlíček, 1968) from the lower Berounian (Sandbian Global Stage) of Bohemia (Libeň and Letná formations) and *S. reticula* (Vinassa de Regny, 1927) from Sardinia (Portixeddu Formation), both recorded from several localities (*e.g.* Villas 1985, Havlíček *et al.* 1987, Leone *et al.* 1991, Gutiérrez-Marco *et al.* 1996a). Villas (1985) discussed the possible synonymy of *S. reticulata* with the type species *S. hibernica* Wright, 1964, due to similarities in the dorsal internal characters. However, the poor preservation of the type material prevents further comparisons. Sayar & Cocks (2013) reported a taxon close to *S. porosa* in the Katian "Pendik Bryozoan Shales" of the western Pontides (NW Turkey), co-occurring with specimens assigned to *S. hibernica.* No pictures of this material are available to confirm its assignment to the Bohemian and Avalonian species. The only external mould found in the Riba de Cima Member was assigned to *Saukrodictya*, but using open nomenclature due to the absence of important internal diagnostic characters.

Dolerorthis Schuchert & Cooper, 1931 has been reported from the Sandbian of Baltica (Norway; Harper *et al.* 1984), the upper Sandbian–lower Katian of the Chu-Ili Range and Chingiz Terrane, Kazakhstan (Klenina *et al.* 1984, Popov *et al.* 2002), the upper Sandbian–lower Katian of Avalonia (Wales; Hurst 1979), the upper Sandbian of the Midland Valley Terrane (Pomeroy, Ireland; Candela 2003); Sandbian of Girvan, Scotland (Williams 1962) and North China (Rong & Zhan 1996). Three species of this genus are known in high-latitude peri-Gondwana, *D. interplicata* (Vinassa de Regny, 1927) and *D. maxima* (Vinassa de Regny, 1927) from the upper Berounian–Kralodvorian (Katian Global Stage) Portixeddu Formation of Sardinia and *D. abeirensis* Mélou, 1990 from the upper Kralodvorian (global uppermost Katian) of the Armorican Massif. *Dolerorthis interplicata* has been reported only from Sardinia. *Dolerorthis maxima* is also present, besides its type strata, in the Pyrenees (Colmenar 2015), the Montagne Noire (Havlíček 1981, Havlíček *et al.* 1987, Leone *et al.* 1991) and the Carnic Alps (Havlíček *et al.* 1987). *Dolerothis abeirensis* occurs in the Armorican Massif and in the Portuguese Central Iberian Zone together with *Kjaerina* (*Villasina*) *meloui* that is one of the species proposed below as index taxon for the upper Kralodvorian.

Havlíček (1950) erected *Bicuspina* based on the species *Orthis cava* Barrande, 1848 of the lower–middle Berounian [Sandbian–lower Katian (Ka1)] of Bohemia. Only two other species of the genus have been described in peri-Gondwana: *Bicuspina multicostellata* Havlíček, 1950 from the uppermost middle Berounian (lower Katian, Ka1) of Bohemia, which is also reported in the middle Berounian [upper Sandbian (Sa2)–lower Katian (Ka1)] of the Moroccan Anti-Atlas (Havlíček 1971) and *Bicuspina armoricana* Mélou, 1990 from the Kralodvorian of the Armorican Massif. The later species is also present in Iberia in both Spain (Gutiérrez-Marco *et al.* 1996a) and

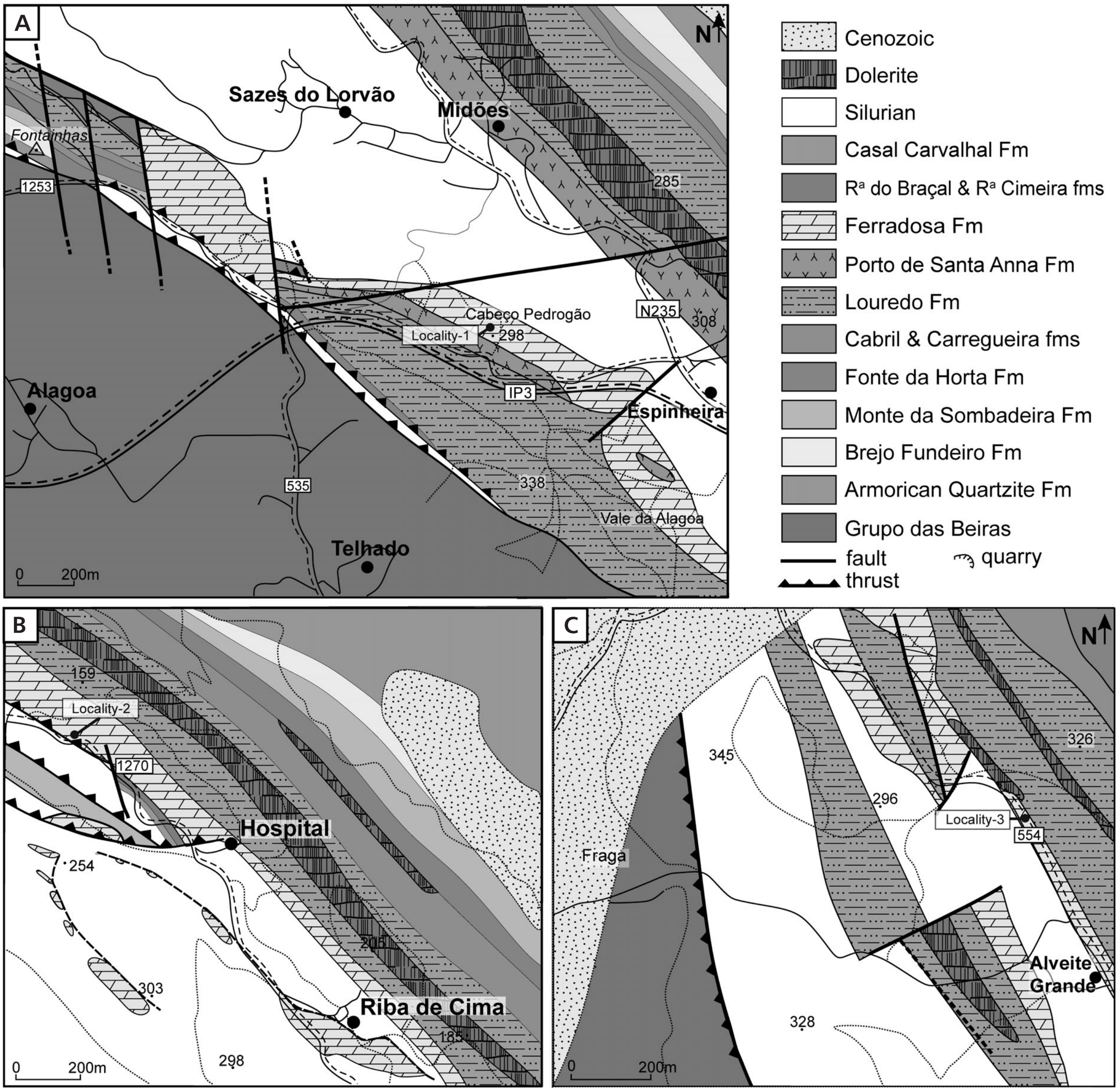


Figure 2. Geological setting of the studied localities. • A – locality 1, Cabeço Pedrogão. • B – locality 2, Ferradosa. • C – locality 3, Alveite Grande.

probably in Portugal (this paper) and, with uncertainty, in the upper Berounian–Kralodvorian of the Carnic Alps and in Sardinia [reported as *B. spiriferoides* by Havlíček *et al.* (1987)]. Apart from peri-Gondwana, this genus is present in the Sandbian of North China (Rong & Zhan 1996); the lower Katian of Laurentia (Candela 2015); the Burrellian (upper Sandbian) of the Midland Valley Terrane (Pomeroy, Ireland; Candela 2003); the Aurelucian–Burrellian (upper Sandbian) of Avalonia (N. Wales; Pickerill & Brenchley 1979); the Sandbian of the Argentinian Precordillera (Benedetto 2003); the upper Sandbian–lower Katian of the Chinghiz Terrane from Kazakhstan (Popov *et al.* 2002) and from the Kukruse stage (lower Sandbian) of Baltica (Estonia; Hints & Rõõmusoks 1997).

Iberomena and *Kjaerina* (*Villasina*) emerge in the peri-Gondwanan realm during the late Berounian and thrived there until the end of the Kralodvorian. So far, the occurrences of these two genera are restricted to the fossil record of this domain (Colmenar 2016, fig. 20). Only one species of *Iberomena* has been described, *I. sardoa* (Vinassa de Regny, 1927), whereas four species have been ascribed to the *Kjaerina* (*Villasina*) subgenus: (1) *Kjaerina* (*V.*) *pedronaensis* Colmenar, 2016, the type species, from the upper Berounian–Kralodvorian of Sardinia and reported here for the first time in the Kralodvorian of Portugal; (2) *Kjaerina* (*V.*) *pyrenaica* Colmenar, 2016 from the upper Berounian of the Pyrenees, Spain; (3) *Kjaerina* (*V.*) *almadenensis* (Villas, 1995) known from the Central Iberian Zone (uppermost "Bancos Mixtos", Spain; lower part of the Porto de Santa Anna Formation, Portugal) and from the Armorican Massif (lower and middle parts of the Rosan Formation, assigned to the upper Berounian–lower Kralodvorian – see discussion in next chapter); and (4) *Kjaerina* (*V.*) *meloui* Colmenar, 2016 from the Kralodvorian of the Armorican Massif (limestones of the upper part of the Rosan Formation), present also in the association studied here. The last two species may be used as key elements for subdividing the Kralodvorian (see next chapter).

Trilobites. – The trilobites from the Riba de Cima Member have not been documented before. During the campaign in the Cabeço Pedrogão locality, in 1897 (Locality 1), three trilobite fossils were collected (Fig. 5A, C, H–J). However, they were neither included in Delgado's (1908) fossil lists nor studied by subsequent researchers. The trilobite fossils of the Riba de Cima Member are scarce and poorly preserved, highly fragmented and exfoliated. For this reason, it is extremely difficult to collect identifiable specimens. This preservational style is very similar to that of some trilobite fossils from other peri-Gondwanan Kralodvorian carbonate rocks, particularly the Cystoid Limestone [Spain, Hammann 1992]. The revision of the Cystoid Limestone Formation material studied by Hammann (1992), housed in the Museo de Ciencias Naturales de la Universidad de Zaragoza (Zaragoza, Spain), led to the identification of the fragmentary Portuguese material, although most of the assignments are made using open nomenclature. In addition, the tentative identification of isolated trilobite sclerites was based not only on direct comparison with the Cystoid Limestone Formation specimens, but also on the knowledge of other trilobites from closely located and probably coeval fossil localities in the Penacova region (*e.g. Ovalocephalus* sp. from Locality 3 and *Parillaenus*? cf. *creber* from Locality 1). The lithostratigraphic context of these other localities needs to be confirmed (they are probably assignable to the Poiares Member of the Ferradosa Formation) and for this reason they were not included in this study.

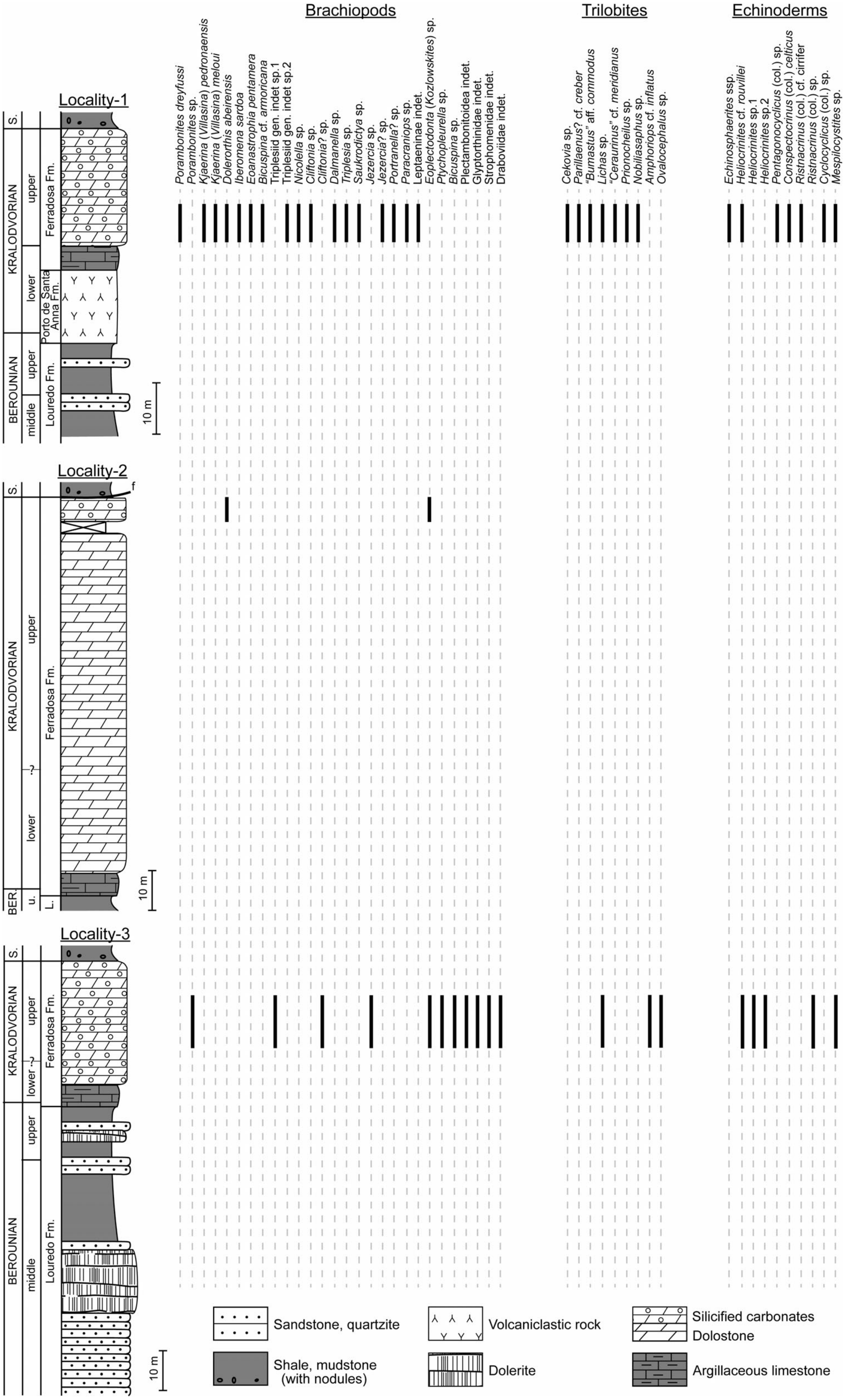
The species *Parillaenus*? *creber* (Hammann, 1992), later assigned by this author to the genus *Illaenus* (Hammann & Leone 1997), probably does not belong to either of these genera. The assignment to the genus *Illaenus* was based on Sardinian material, considered by Hammann & Leone (1997) as conspecific with the Spanish type-material. We prefer to maintain the first doubtful generic assignment to *Parillaenus*, a genus with the Baltic origin. The main diagnostic dorsal characters and the hypostome configuration suggest a close relationship to *Parillaenus* (as discussed by Hammann 1992, pp. 57–59). In the course of this study, only isolated sclerites were found (Fig. 5B), but the presence of better preserved material in the Poiares Member, 100 meters west of Locality 1 and in the uppermost Kralodvorian of the Porto de Santa Anna Formation (Colmenar *et al.* 2016), supports the assignment to *P.*? *creber.* Regardless of generic assignment, the species *P.*? *creber* and related Portuguese and Sardinian specimens represent a morphological group of illaenids characteristic for Kralodvorian assemblages of High-Latitude peri-Gondwana, and no closely related form is known from older rocks of this realm. Therefore, the occurrence of these illaenids probably represents a Baltic immigration related to the Boda Event.

Despite the previous assignment of several species from South China to *Cekovia* (Zhou & Zhou 2008 and references therein), an ongoing revision of this genus led to the rejection of their generic assignment. The genus *Cekovia* is here considered to be endemic to the High-Latitude peri-Gondwana realm. The oldest record of this genus is *C. transfuga* (Barrande 1852), from the lower Berounian (Sandbian in the global scale) of the Libeň Formation of the Czech Republic, with *C. salteri* from the middle Berounian (*ca.* upper Sandbian–lower Katian) of the Zahořany Formation, presenting the youngest known record in Bohemia (*e.g.* Bruthansová 2003). However, during the Kralodvorian (upper Katian) *Cekovia* is one of the most common trilobites in the echinoderm-dominated assemblages of the carbonate units of Ibero-Armorica, *i.e.* in Portugal (this work), Spain (Robardet 1976, Hafenrichter 1979, Hammann 1992), France (Kerforne 1901, Lebrun 2002) and also in Morocco (Villas *et al.* 2016). *Cekovia* sp. (Fig. 5D–E) from the Riba de Cima Member is the first record of this genus in the Kralodvorian of Portugal, and is the most abundant trilobite taxon in this unit.

Amphoriops Hammann & Leone, 1997 was defined as a subgenus of *Thaleops* Conrad, 1843, but as suggested by Amati & Westrop (2006) it, most probably, represents an independent genus. *Amphoriops* was previously known only from the Kralodvorian of Spain and Sardinia, represented by the species *A. inflatus* (Hammann, 1992) and *A. zoppii* (Hammann & Leone, 1997). Only a single cranidium (Fig. 7S–T) was collected from the Riba de Cima Member, and was (with reserve) assigned to the type-species *Amphoriops inflatus* known from the Cystoid Limestone Formation, Kralodvorian (upper Katian) of Spain [also documented in the Portixeddu Formation, Katian of Sardinia (Hammann & Leone 1997)].

In the high-latitude peri-Gondwanan realm, bumastiform trilobites are only known in the Kralodvorian (Hammann 1992). In the Kralodvorian Cystoid Limestone Formation, Hammann (1992) documented "*Bumastus*" aff. *commodus* Apollonov, 1980, to which taxon the pygidia

Figure 3. Logs of the studied localities with the stratigraphic ranges of the species. • A – locality 1, Cabeço Pedrogão – Sazes do Lorvão. • B – locality 2, Ferradosa, after Young (1988). • C – locality 3, Alveite Grande.



from the Riba de Cima Member (Fig. 5C) are tentatively assigned. The generic assignment of the Spanish specimens was thoroughly discussed by Hammann (1992, p. 80). The material from Portugal and Spain bears resemblance with *Bumastus commodus* from the uppermost Katian Tschokparsk 'Horizon' from Kazakhstan. This is the first record of a bumastiform trilobite in Portugal.

The oldest worldwide known record of the genus *Lichas* Dalman, 1827 comes from the middle Berounian (*ca.* upper Sandbian–lower Katian) of Portugal (see Pereira *et al.* 2015b). A high-latitude peri-Gondwanan origin was suggested for this genus (Pereira *et al.* 2015b), although the fact that *Lichas* was first described from Baltica apparently justifies it being considered as Baltic (*e.g.* Hammann 1992). During the upper Katian, probably related to the global reduction of endemism (the Boda Event), *Lichas* expanded its geographic distribution, reaching Avalonia and Baltica. Later it became a cosmopolitan genus frequently present in Hirnantian assemblages (*Hirnantia* Fauna assemblages). This genus is very common in the Kralodvorian trilobite assemblages of the High-Latitude peri-Gondwanan realm which are dominated by illaenids, cheirurids and lichids. In the fossil record of this region, besides the Riba de Cima Member (Figs 3F, G, 5W), the genus was documented as being common in other Kralodvorian (upper Katian) carbonate units of Spain (Cystoid Limestone Formation; Hammann 1992) and Sardinia (Portixeddu Formation; Hammann & Leone 1997).

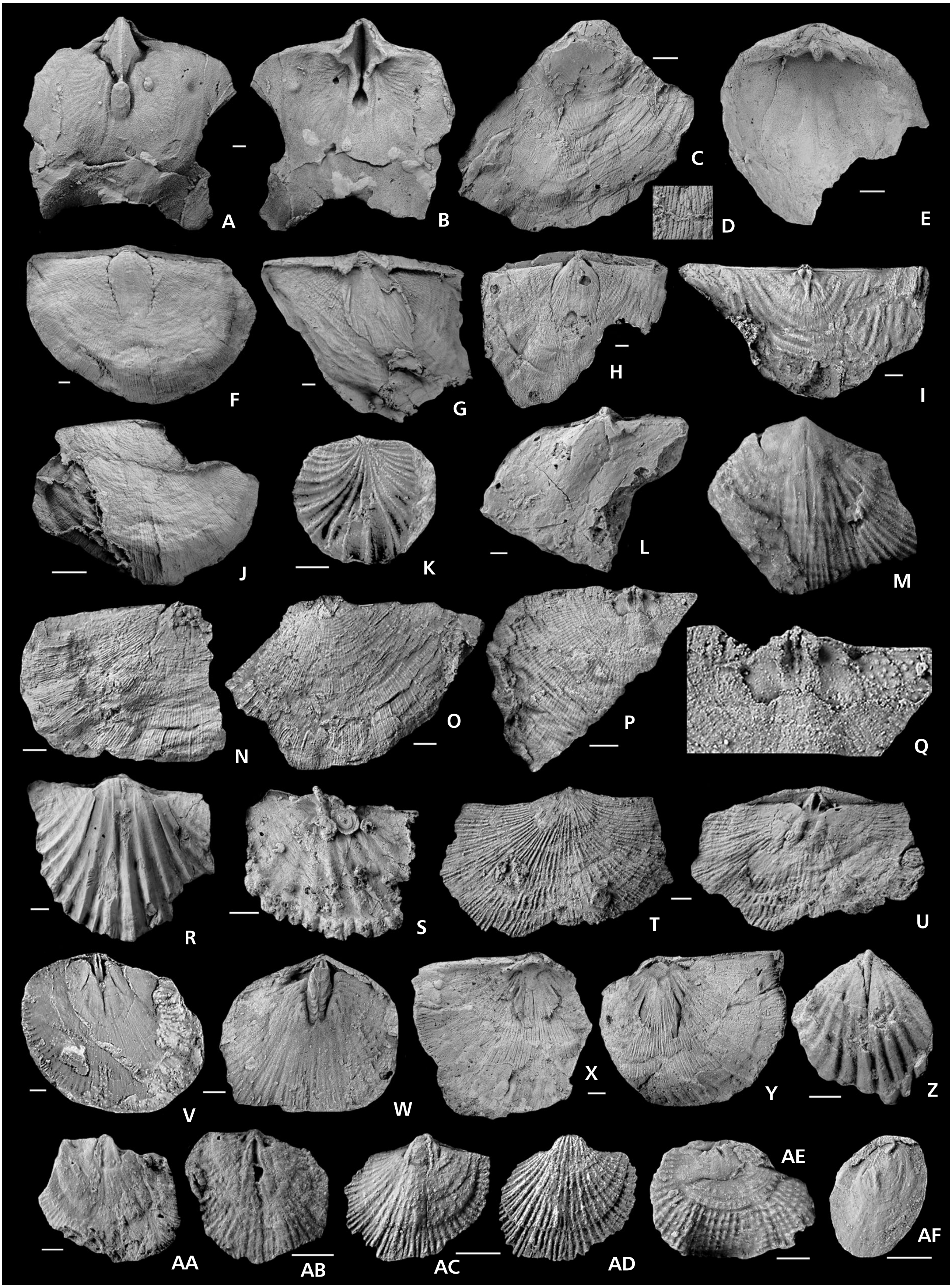
A single cranidium (Fig. 5H–J) is here identified as "*Ceraurinus*" cf. *meridianus* (Hammann 1992), a taxon previously documented only in the Kralodvorian Cystoid Limestone Formation of Spain. This species was originally assigned to the genus *Cyrtometopus* (see Hammann 1992, p. 98). This generic assignment is here rejected, based on the more posterior location of the palpebral lobes and non-parallel-sided glabella of the Spanish species. "*Ceraurinus*" cf. *meridianus* is related to *Ceraurinus*-like [*sensu* Pärnaste 2008] genera, probably representing a new Cyrtometopinae genus. The *Ceraurinus*-group genera have their oldest record in the Lower Ordovician of Baltica, but in High-Latitude peri-Gondwana it was recorded in the Kralodvorian only. Therefore, the presence of "*Ceraurinus*" cf. *meridianus* in the Riba de Cima Member fossil record is certainly related to the faunal exchanges of the Boda Event, as previously suggested by Hammann (1992).

The Riba de Cima Member of the Ferradosa Formation provided one sole librigena identified as *Ovalocephalus* sp. This generic identification is based on the comparison with dozens of well-preserved specimens assigned to *Ovalocephalus tetrasulcatus* (Kielan, 1960) in the Poiares Member (the lower member of the same formation). This species was documented in the upper Katian of Baltica (Poland; Kielan 1960) and peri-Gondwana (Portugal; this paper), Spain (Hammann 1992), Sardinia (Hammann & Leone 2007) and Turkey (Dean & Zhou 1988). The conspecific assignment of specimens of *Ovalocephalus* from China, Kazakhstan, and Kyrgyzstan by Zhou *et al.* (2010) is considered doubtful, bearing slightly larger L1, adaxially defined by shallower furrows.

Ovalocephalus probably arose in South China, where the genus is known from the Floian (Lower Ordovician), and extended its geographical distribution in successive transgressive events (Zhou *et al.* 2010). During the upper Katian, with the decreasing endemicity related to the Boda Event, *Ovalocephalus* became widespread throughout the high-latitude peri-Gondwanan area into the Kazakh terranes and Shibumasu (Portugal, Spain, Sardinia, Turkey, Uzbekistan, Kazakhstan, Kirgizstan, Mongolia and Thailand) and also in Baltica (Poland). In the high-latitude peri-Gondwana, *Ovalocephalus* is only known from Kralodvorian units (Cystoid Limestone Formation, Spain; the Punta S'Argiola Member of Domusnovas Formation; and the Tuviois Formation, Sardinia), all considered coeval with the Ferradosa Formation.

Finally, a thoracopygon identified as *Prionocheilus* sp.

Figure 4. Brachiopods from the Riba de Cima Member, upper Kralodvorian (upper Katian) at Locality 2, Cabeço Pedrogão, Sazes do Lorvão (Penacova). • A–D – *Porambonites dreyfussi* Havlíček, 1981; A–B – ventral valve internal mould (A) and latex cast of the interior (B), MG3214; C–D – latex cast of the exterior (C) and detail of the fenestrate ornament (D) of an indeterminate valve, MG30650. • E – Triplesiidae gen. et sp. nov. 2, latex cast of dorsal valve interior, MG30651. • F–J – *Kjaerina* (*Villasina*) *pedronaensis* Colmenar, 2016; F, J – ventral valve internal mould (F) and latex cast of exterior (J), MG30651; G – latex cast of ventral valve interior, MG3219; H – ventral internal mould, MG30652; I – latex cast of the interior of a dorsal valve, MG30653. • K – *Portranella*? sp. – latex cast of dorsal valve exterior, MG30654. • L–M – *Bicuspina* cf. *armoricana* Mélou, 1990. L – ventral valve internal mould, MG30655; M – dorsal valve internal mould, MG30656. • N–Q – *Kjaerina* (*Villasina*) *meloui* Colmenar, 2016; N – ventral valve internal mould, MG30657; O – latex cast of ventral valve exterior, MG30658; P–Q – latex cast of dorsal valve interior (P) and detail of the cardinalia with the meso-cardinal ridge (Q), MG30659. • R–S – *Nicolella* sp.; R – ventral valve internal mould, MG30660; S – latex cast of dorsal valve interior, MG30661. • T–U – *Dolerorthis abeirensis* Mélou, 1990, latex cast of exterior (T) and internal mould (U) of a dorsal valve, MG30662. • V–W – *Dalmanella* sp.; V – dorsal valve internal mould, MG3224; W – ventral valve internal mould, MG30663. • X–Y – *Iberomena sardoa* (Vinassa de Regny, 1927), latex cast of interior (X) and internal mould (Y) of a dorsal valve, MG30664. • Z – *Eoanastrophia pentamera* (Meneghini, 1857), dorsal valve internal mould, MG30665. • AA–AD – *Jezercia*? sp.; AA – ventral valve, internal mould, MG30666; AB – dorsal valve, internal mould, MG30667; AC–AD – ventral valve internal mould (AC) and latex cast of exterior (AD), MG3068. • AE – *Cliftonia*? sp., ventral valve internal mould, MG30669. • AF – *Paracraniops* sp., ventral valve, internal mould, MG30670. Scale bars represent 2 mm.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(Fig. 5A) and an exfoliated fragment of *Nobiliasaphus* sp. (Fig. 5K) were also collected. The genera *Prionocheilus* and *Nobiliasaphus* are both considered to have originated in the High-Latitude peri-Gondwana realm, being common in its fossil record from the Lower and the Middle Ordovician, respectively, through to the Kralodvorian (*ca.* upper Katian). During the late Darriwilian–early Katian, *Prionocheilus* expanded its geographical distribution to Baltica [*e.g. P. nieszkowskii* (Schmidt, 1894) of Estonia, and *P. foveolatus* (Törnquist, 1884) of Sweden] and to China (*e.g. P. parapulchra* Kobayashi, 1951), and during the upper Katian the genus reached other regions, such as Avalonia (*e.g. P. cautleyensis* Ingham, 1977, from the Cautley Mudstone Formation, Cumbria, England), the Kazakh terranes [*e.g. P. inermis* Kolobova *in* Sokolov & Yolkin (1978), of the Obikalon Member of the Shakhriomon Formation, Uzbekistan, and *P. solitus* Apollonov 1974 of the upper Katian?–Hirnantian of Kazakhstan]. In the Kralodvorian rocks of High-Latitude peri-Gondwana, *Prionocheilus* has been previously documented in Spain [*P. obtusum* (M'Coy, 1846), Cystoid Limestone Formation] and in Sardinia [*P. inermis* Kolobova *in* Sokolov & Yolkin, (1978), Portixeddu Formation and *P. rutilus* Hammann & Leone, 1997, Cyclopygid Bed of the Punta S'Argiola Member of the Domusnovas Formation].

The trilobite association of the Riba de Cima Member of the Ferradosa Formation supports the assignment of this unit to the Kralodvorian (*ca.* upper Katian). Several taxa are documented in Portugal for the first time: *Parillaenus*? cf. *creber, Amphoriops* cf. *inflatus*, "*Bumastus*" aff. *commodus*, "*Ceraurinus*" cf. *meridianus* and *Ovalocephalus* sp. All of them are exclusively known from the Kralodvorian of high-latitude Gondwana (with the exception of *Ovalocephalus*, but the specific identification of *O. tetrasulcatus* in the Poiares Member also limits its range to the Kralodvorian). In Ibero-Armorica, these five taxa were previously documented from the Cystoid Limestone Formation of Spain (Hammann 1992) only. The remaining identified trilobites (*Cekovia* sp., *Lichas* sp., *Prionocheilus* sp. and *Nobiliasaphus* sp.) also characterize the Kralodvorian assemblages of this region. It is important to highlight that the Kralodvorian trilobite assemblages of the high-latitude peri-Gondwanan realm (specially from Ibero-Armorica and Morocco), although bearing some taxa considered to have originated in other regions (namely Baltica, Kazakh terranes and South China), were still composed largely by hitherto endemic representatives (*e.g. Cekovia, Lichas, Prionocheilus, Nobiliasaphus,* as discussed above). Some of these peri-Gondwana trilobite taxa expanded their geographical distribution during the late Katian, with their faunal shifts being coeval with the "poleward invasion" (*sensu* Fortey & Cocks 2005) related to the Boda Event. This trilobite "reverse invasion" has been overlooked in previous works (*e.g.* Hammann 1992, Fortey & Cocks 2005) as a result of different generic assignments and/or inaccurate determination of the region where they evolved, with some taxa now considered peri-Gondwanan in origin (*e.g. Lichas, Radnoria, ?Ulugtella*; Pereira *et al.* 2015a, b).

Problematic issues on the Kralodvorian Regional Stage and its redefinition

The Kralodvorian Regional Stage was established by Havlíček & Marek (1973), originally as a series of regional status, corresponding to the Králův Dvůr Formation. Its lower boundary with the underlying upper Berounian was defined by a sharp change in sedimentation and faunal community at the base of the Králův Dvůr Formation (Fatka *et al.* 1995) representing possible deepening of the Prague Basin.

The validity of the Kralodvorian Regional Stage has been questioned by Kraft *et al.* (2015). They argued that the Kralodvorian represents a specific and probably heterochronous succession of facies and faunal associations that reflect distinct conditions widespread in peri-Gondwanan Europe (and Gondwanan North Africa) at that time, clearly different from those of the underlying and overlying units. Gutiérrez-Marco *et al.* (2017) agreed with Kraft *et al.* (2015) that these criteria are irrelevant for the definition of a formal chronostratigraphic unit, but they highlighted that those criteria are extremely useful for inter-regional correlations between successions with a scarcity or absence of graptolites, long ranging conodont zones, or inconclusive data obtained from other groups.

Kraft *et al.* (2015) provided new graptolite data and proposed a tentative correlation of the Králův Dvůr Formation with the regional British and global stages. The first key taxon is the graptolite *Anticostia teres* that probably occurs in the basal Podolí 'Horizon' of the Králův Dvůr Formation, but it has certainly been found in the following metres of overlying black shales in the lower part of the formation. This taxon occurs in *Pleurograptus linearis* Zone strata in Baltica (Bornholm and Sweden) (Kraft *et al.* 2015). However, since the range of the *P. linearis* Biozone in England and Wales (Ka2–Ka3) extends from the regional uppermost Caradoc until (at least) the middle part of the Rawtheyan Substage of the type Ashgillian (Rickards 2002, 2004; Zalasiewicz *et al.* 2009), the correlation proposed by these authors with the Caradoc-Ashgill boundary of the regional British scheme has been considered imprecise (Gutiérrez-Marco *et al.* 2017). Štorch & Mergl (1989) placed the Kralodvorian-Kosovian boundary in the Prague Basin by the sudden extinction of the high diversity *Proboscisambon* Community ("Perník Bed") and

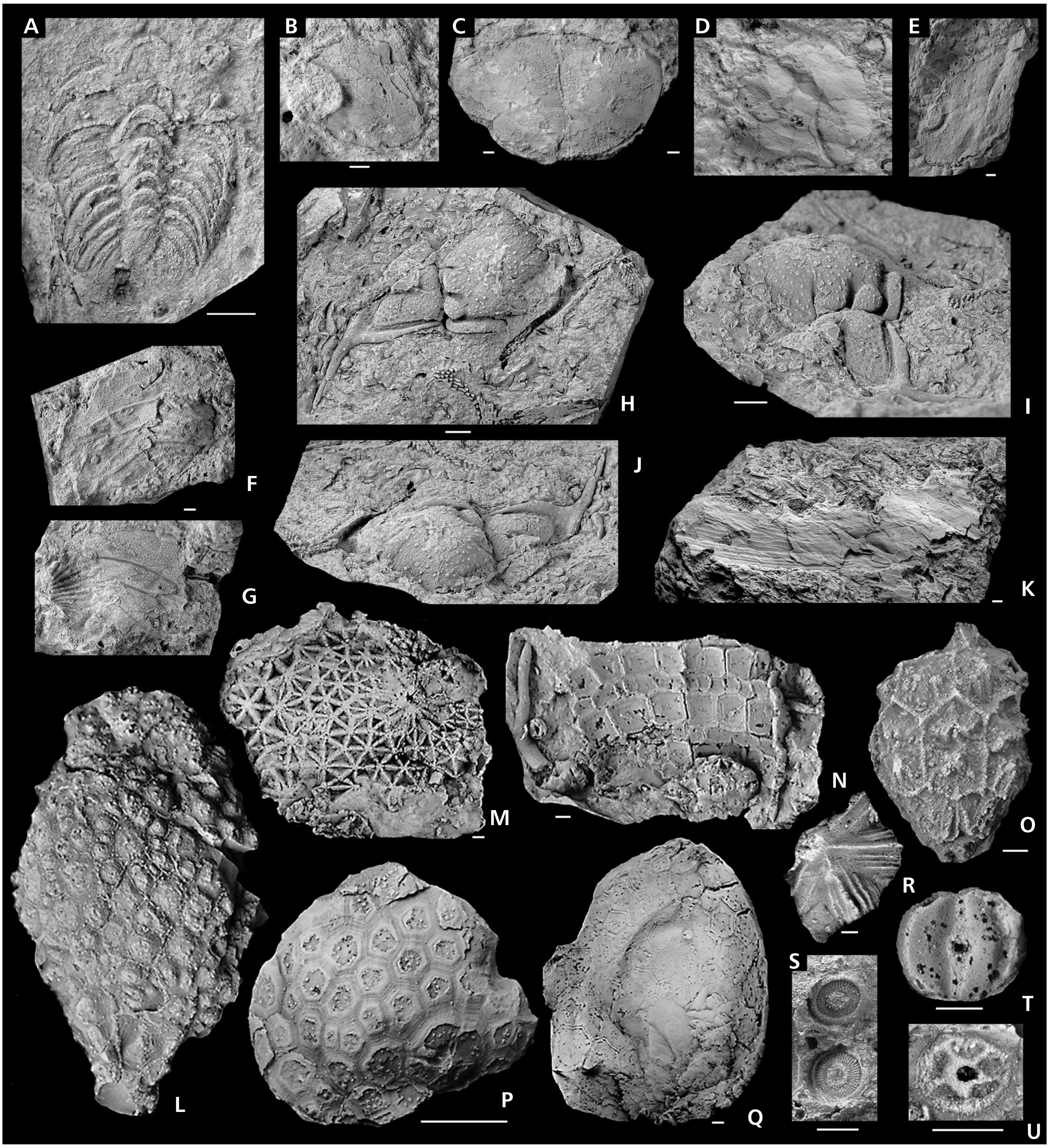


Figure 5. Trilobites and echinoderms from the Riba de Cima Member, upper Kralodvorian (upper Katian) at Locality 2, Cabeço Pedrogão, Sazes do Lorvão (Penacova). • A – *Prionocheilus* sp., internal mould of a thoracopygon, MG3205. • B – *Parillaenus*? *creber* (Hammann, 1992), internal mould of a librigena, MG15711. • C – *"Bumastus"* aff. *commodus* Apollonov, 1980, internal mould of a pygidium, MG3271. • D – *Cekovia* sp., internal mould of a cranidium, MG30585. • F–G – *Lichas* sp., external mould (F) and internal mould (G) of a fragment of a pygidium, MG30626. • H–J – "*Ceraurinus*" cf. *meridianus* Hammann, 1992, internal mould of a cranidium in dorsal (H), lateroblique (I) and anteroblique (J) views, MG170. • K – *Nobiliasaphus* sp., internal mould of an exfoliated fragment, MG30576. • L, P–Q – *Echinosphaerites* spp.; internal mould of an elongated theca with variably sized and irregular in outline plates (L), MG3236; internal mould of a theca (P), MG3231a; internal mould of a theca (Q), MG3231b. • M – *Heliocrinites* cf. *rouvillei* von Koenen, 1886, latex cast of a theca, MG3232. • N – Diploporita indet., latex cast of a fragment of theca showing primary and secondary plate cycles, MG3236. • O – Hemicosmitida indet., complete silicified theca in lateral view, MG30671. • R – *Macrocystella* sp., latex cast of an incomplete thecal plate, MG3233. • S – *Pentagonocyclicus* (col.) sp., external mould of two disarticulated columnal plates, MG30672. • T – *Ristnacrinus* (col.) cf. *cirrifer* Le Menn, 1973, latex cast of a columnal plate, MG3241. • U – *Conspectocrinus* (col.) *celticus* Le Menn, 1973, latex cast of a columnal plate, MG3245. Scale bars represent 2 mm.

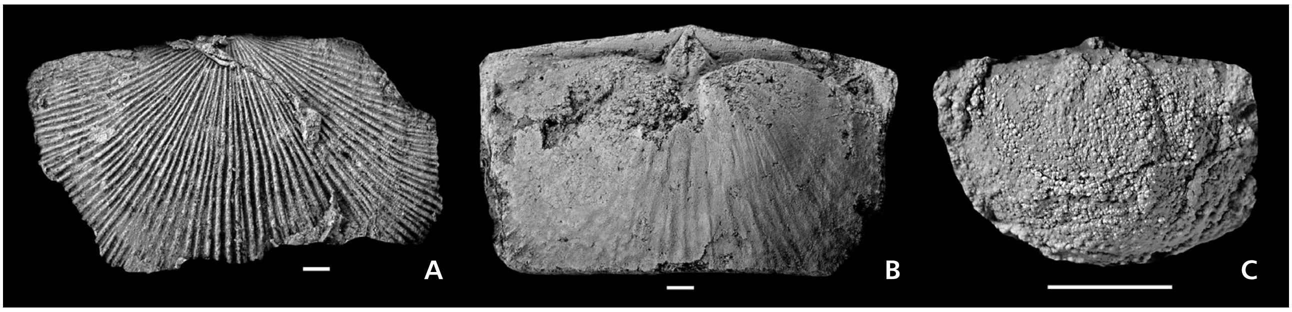
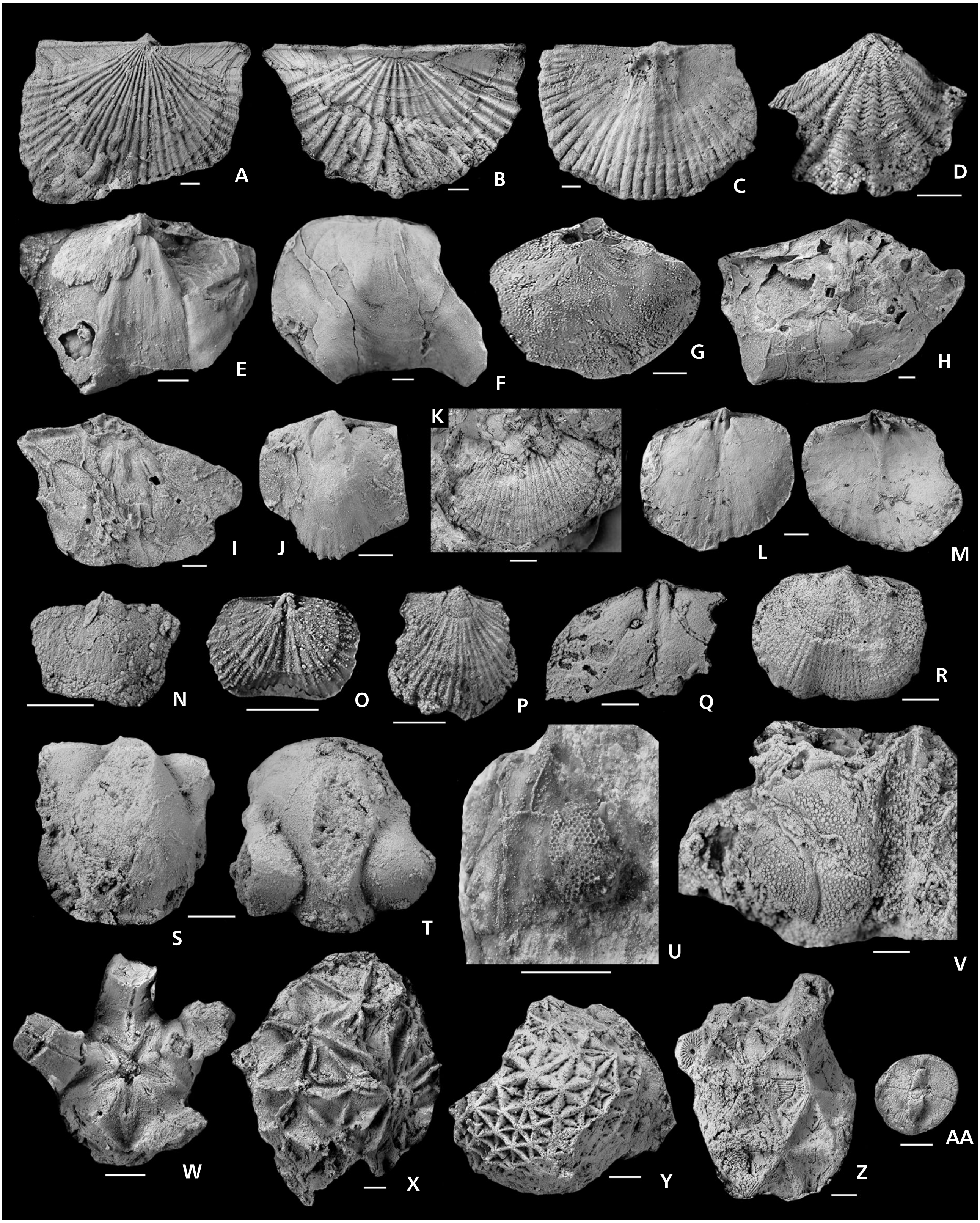


Figure 6. Brachiopods from the Riba de Cima Member, upper Kralodvorian (upper Katian) at Locality 3, Ferradosa (Penacova). • A–B – *Dolerorthis aberirensis* Mélou, 1990, latex cast of the exterior (A) and internal mould (B) of a dorsal valve, MG30673. • C – *Eoplectodonta* (*Kozlowskites*) sp., internal mould of a ventral valve, MG30674. Scale bars represent 2 mm.

its replacement by the *Mucronaspis* Community in the overlying bed. These faunistic replacements, together with the drastic lithological changes recorded in the basin, related with the onset of the Hirnantian glaciation, allowed Štorch & Mergl (1989) to correlate the Kralodvorian-Kosovian boundary with the Anglo-Scandic Rawtheyan-Hirnantian boundary. Thus, Štorch (1990) placed the Kralodvorian-Kosovian boundary just above the "Perník Bed", criteria followed by several authors since then to place the Katian-Hirnantian boundary (Mergl 2011a, Kraft *et al.* 2015). The presence of *Metabolograptus ojsuensis* (indicative of the Hirnantian *sensu* Kraft *et al*. 2015) in the Králův Dvůr Formation is also relevant; its first occurrence is at the basal layer of the shale overlying the "Perník Bed" which marks the upper limit of the Kralodvorian (Kraft *et al*. 2015). However, the first occurrence of typical *Hirnantia* Fauna in the Barrandian area has been registered in the topmost Králův Dvůr Formation (Mergl 2011a), in levels slightly above the occurrence of the *Mucronaspis* Community. In addition, Mitchel *et al.* (2011) detected a positive peak in $\delta^{13}C_{org}$ in the shale interval between the top of the "Perník Bed" and the diamictite at the base of the overlying Kosov Formation, which has been interpreted as the Hirnantian Isotopic Curve Excursion (HICE). Mergl (2011b), after a taphonomical study of the small bioclasts of the "Perník Bed", suggesting that all bioclasts were transported in higher or lesser extent, interpreted this bed as a result of the deposition of a distal mudflow, which brought fine bioclasts into deeper parts of the basin, related with the effects of a glacio-eustatic sea level drop. This interpretation suggests that the "Perník Bed" deposition should be likely isochronous with the onset of the Hirnantian glaciation, and thus, if this is true the upper limit of the Kralodvorian would lie above the Katian-Hirnantian boundary. The fauna occurring in the "Perník Bed", the *Proboscisambon* Fauna (Štorch & Mergl 1989), which corresponds to the small sized *Foliomena* Fauna (Harper 1979), is typical from deep environments (BA4–BA5 or deeper; Rong *et al.* 1999 and references therein). Also larger size taxa occur such as the brachiopods *Eoanastrophia* and *Hindella* and the trilobites *Mucronaspis, Duftonia, Actinopeltis, Gravicalymene, Octillaenus, Marekolithus*, rarely complete. An alternative, and in our opinion, more plausible explanation is that the bioclasts of the "Perník Bed" were transported basinward just by simple marine flows or transport downslope the platform, and then accumulated in deep environments bearing a mixture of big brachiopod and trilobite remains (always fragmented or incomplete), probably originally from shallower environments [*Eoanastrophia* is a characteristic genus of the *Nicolella* Fauna, lower BA3 (Colmenar 2016); *Hindella* is a genus usually present in BA2–upper BA3 benthic assemblages (Rong & Harper 1988); *Actinopeltis* and *Octillaenus* are usually associated

Figure 7. Brachiopods, trilobites and echinoderms from the Riba de Cima Member, upper Kralodvorian (upper Katian) at Locality 4, Alveite Grande (Vila Nova de Poiares). • A–C – *Nicolella* sp.; A – latex cast of dorsal valve exterior, MG30675; B – latex cast of dorsal valve exterior, MG30676; C – dorsal valve interior, MG30677. • D – *Ptychopleurella* sp., latex cast of a dorsal valve exterior showing the characteristic lamellate ornament of this taxon, MG30678. • E – *Bicuspina* sp. internal mould of an incomplete ventral valve with part of the shell preserved, MG30679. • F–G – *Triplesia* sp.; F – internal mould of a ventral valve, MG30680; G – internal mould of a dorsal valve, MG30681. • H – Strophomenidae indet., internal mould of a dorsal valve, MG30682. • I – *Iberomena sardoa* (Vinassa de Regny, 1927), internal mould of a dorsal valve, MG30683. • J–M – *Dalmanella* sp.; J – internal mould of a ventral valve, MG30684; K–M – latex cast of exterior (K), internal mould (L) and latex cast of interior (M) of a dorsal valve, MG30685. • N – Plectambonitoidea indet. internal mould of a ventral valve, MG30686. • O–P – *Jezercia* sp.; O – internal mould of a dorsal valve, MG30687; P – internal mould of a ventral valve, MG30688. • Q – Draboviidae indet. – internal mould of an incomplete dorsal valve, MG30689. • R – *Cliftonia*? sp. ventral valve with the shell preserved, MG30690. • S–T – *Amphoriops* cf. *inflatus* (Hammann, 1992), internal mould of a cranidium in anteroblique (S) and dorsal (T) views, MG30612. • U – *Ovalocephalus* sp., internal mould of a librigena with the eye preserved, MG30574. • V – *Lichas* sp., internal mould of an incomplete cranidium, MG30575. • W – *Mespilocystites* sp., latex cast of a complete specimen in oral view, MG30691. • X – *Heliocrinites* sp. 1, latex cast



of an incomplete theca in lateral view, MG30692. • Y – *Heliocrinites* cf. *rouvillei* von Koenen, 1886, latex cast of an incomplete theca in lateral view, MG30693. • Z – *Heliocrinites* sp. 2, latex cast of an incomplete theca in lateral view showing the proximal part of one arm, MG30694. • AA – *Ristnacrinus* (col.) sp., latex cast of a columnal plate, MG30695. Scale bars represent 2 mm.

with taxa that characterizes the Cheirurid-Illaenid Community, typical of shallow shelf environments (Hammann & Leone 2007)], together with deep-water fauna (*Foliomena* Fauna and small trilobites) also probably partially transported downslope. This downslope transportation was also previously proposed for bryozoans (Mergl 2011b). With this simple explanation the Katian-Hirnantian boundary is reasonable to be placed, as both faunistic and isotopic evidences suggest (Štorch & Mergl 1989, Štorch 1990, Mergl 2011a, Mitchell *et al.* 2011, Kraft *et al.*2015), in the above the "Perník Bed".

All these data discussed above, indicate that the Kralodvorian Regional Stage, as it is used in modern chronostratigraphy (Gutiérrez-Marco *et al.* 2017), does not necessarily coincide with the Králův Dvůr Formation.

The lowermost Králův Dvůr Formation is characterized by a discontinuous oolitic ironstone horizon, the "Podolí Ore Horizon". This horizon has yielded a very scarce and poorly known trilobite association. Budil *et al.* (2011, p. 4) suggested that there is an apparent mixing of species, with "…survivals from the underlying Bohdalec Formation combined with the late Katian taxa [*Onnia* cf. *ultima*, *Chlustinia mikulasi* (= *keyserlingi fide* Vaněk & Valíček 2001), *Selenopeltis* sp., *Octillaenus*? sp., *Actinopeltis* cf. *gryphus*, *Duftonia juspa konika nomen nudum*… and *Kloucekia* sp.]". However, *Onnia, Chlustinia* and *Duftonia*? *juspa* Šnajdr, 1982 are already present in the upper Berounian Bohdalec Formation (Vaněk & Vokáč 1997), represented by species which are morphologically very similar to the ones listed by Budil *et al.* (2011). In addition, all trilobite specimens from the "Podolí Ore Horizon" are generally poorly preserved and do not enable definitive determination. In our opinion, the trilobites from the Podolí 'Horizon' actually constitute rather an upper Berounian assemblage, as previously indicated by Budil *et al.* (2011). This discontinuous "horizon" also yielded a low diversity brachiopod assemblage (Mikuláš 1985, Havlíček *in* Chlupáč *et al.* 1998), with *Aegiromena*, *Jezercia* and *Gelidorthis*, typical elements of the brachiopod *Aegiromena-Drabovia* Fauna (Havlíček, 1982) widely represented in the upper Berounian Bohdalec Formation. The brachiopod *Leptaena*, also present in this "horizon", is unknown in older Berounian rocks of the Bohemian area (M. Mergl personal communication). Above this horizon, the Králův Dvůr sequence is dominated by the "deeper water" *Rafanoglossa* Community, being the most abundant the brachiopods *Rafanoglossa* and *Chonetoidea* and the trilobites *Amphitryon*, *Kloucekia*, *Flexicalymene*, *Tretaspis*, *Dionide* and some cyclopygids and illaenids. About 20–30 metres below the "Perník Bed", in the upper half of the Králův Dvůr Formation at the Levín section, *Foliomena folium*, *Dedzetina* and *Eoplectodonta* (*Kozlowskites*), characteristic brachiopods of the *Foliomena* Fauna, occur for the first time (M. Mergl personal communication). These brachiopods sometimes co-occur with *Rafanoglossa* specimens (M. Mergl personal communication). Above the *Foliomena folium* bearing beds, *Chonetoidea* and several trilobites such as *Ampyx, Tretaspis, Zetillaenus,* cyclopygids and others occur (M. Mergl personal communication). After few meters of greenish shales without fauna and few centimetres below the Hirnantian Kosov Formation, at the "Perník Bed," the *Proboscisambon* Fauna occurs. As we mention above, this fauna corresponds as well to the deep water *Foliomena* Fauna. Just above the "Perník Bed" in the grey-green claystones and in siltstones of the very last centimetres (*ca.* decimetres to metres of succession in total) of the formation, were identified two distinct fossil associations: one known as the *Mucronaspis* Fauna (Štorch & Mergl 1989), occurring in the claystones, and the other assigned to the *Hirnantia* Fauna, described by Mergl (2011a) in the siltstones 5–7 cm below the diamictite at the base of the overlying Kosov Formation (Kraft *et al.* 2015).

Besides the lithological and facies changes, the disappearance of the brachiopods of the *Aegiromena-Drabovia* Fauna was one of the criteria chosen for the definition of the Kralodvorian Regional Stage (Havlíček & Marek 1973). After the occurrence of these clearly upper Berounian taxa at the basal horizon of the Králův Dvůr Formation, and by the occurrence near the top of the *Hirnantia* Fauna, the limits designated for the Kralodvorian Regional Stage must be reassessed. Here we propose the use of the top of the Podolí 'Horizon', the last level with upper Berounian taxa, as the lower limit of the Kralodvorian in the Bohemian area. When the "Podolí Ore Horizon" is not present at the base of the Králův Dvůr Formation, the LAD (Last Appearance Datum) of the *Aegiromena-Drabovia* brachiopod fauna and the Berounian-like trilobites will mark the top of the Berounian. In addition, we propose the top of the "Perník Bed," as we discussed above, as the upper limit, supported by the occurrence of Hirnantian graptolites and brachiopods above this bed.

In other High-Latitude peri-Gondwanan areas the deepening that occurred in the Bohemian area, marking the beginning of the Kralodvorian, is not recorded. Instead, the Kralodvorian may be recognized by the development of carbonate platforms (*e.g.* southwestern and central Europe, the Ghadamis Basin of Libya and the eastern Tafilalt region of the Moroccan Anti-Atlas; Gutiérrez-Marco *et al.* 2017 and references therein), replacing the previously siliciclastic-dominated platforms. This sedimentary change is interpreted as having been caused by the late Katian global warming Boda Event (Fortey & Cocks 2005) and its related factors, such as increase of water temperatures, rise of sea level and development of high-latitude carbonate platforms (Colmenar 2015) that flooded extensively flat emerged areas interrupting the siliciclastic input.

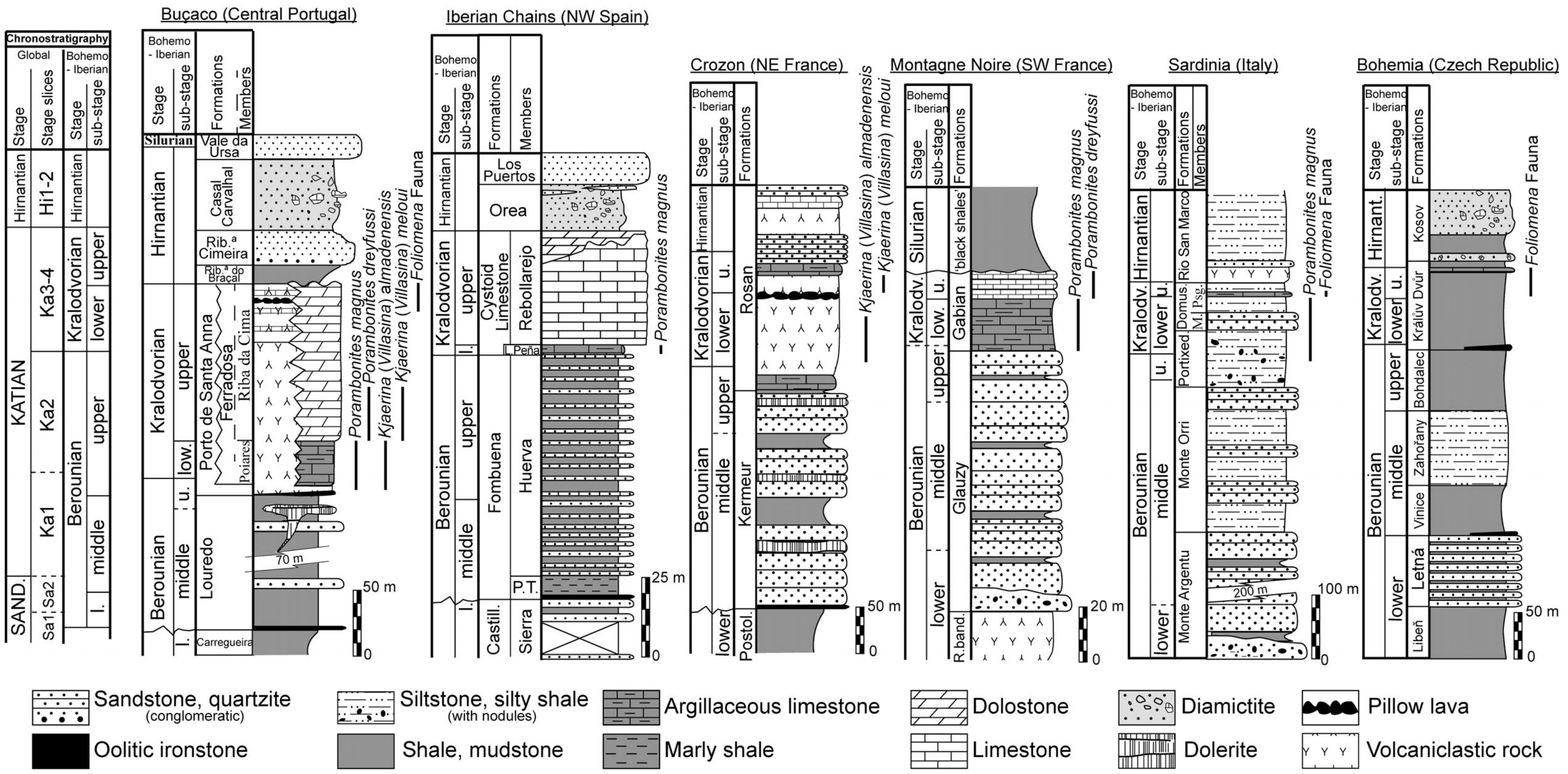


Figure 8. Schematic chronostratigraphic correlation chart among the most relevant sections through western peri-Gondwana showing the stratigraphical ranges of the key taxa. Buçaco log after Sá *et al.* (2011); Iberian Chains log after Cole *et al.* (2017); Crozon log after Caroff *et al.* (2009); Montagne Noire log after Colmenar *et al.* (2013); Sardinia log after Villas *et al.* (2002a); Bohemia log after Havlíček (1977). Abbreviations: l. and low. – lower; u. – upper; SAND. – Sandbian; Rib.^{a} – Ribeira; L. Peña – La Peña Member; Castill. – Castillejo Formation; P.T. – Peña del Tormo Member; Postol. – Postolonnec Formation; Kralodv. – Kralodvorian; Hirnant. – Hirnantian; R. Band. – Roque de Bandies Formation; Portixed. – Portixeddu Formation; Domus. – Domusnovas Formation; M. – Maciurru Member; Psg. – Punta S'Argiola Member.

Shifts of the brachiopod fauna have been also detected in this realm that are marked by the appearance of taxa with low-latitude origins (roughly the *Nicolella* Fauna), which replaced progressively, during the Kralodvorian, the typical endemic biotas (characterized by aegiromenids, draboviids and heterorthids) that inhabited the high-latitude peri-Gondwana during the upper Berounian. However, among trilobites these faunal exchanges seem to have been different, with the arrival of low-latitude taxa being coeval with the geographical expansion of high-latitude Gondwanan trilobites to other domains including Avalonia, Baltica, the Kazakh terranes and South China.

The arrival of the *Nicolella* Fauna in high-latitude peri-Gondwana seems to have been diachronous, controlled by ecological conditions (Gutiérrez-Marco *et al.* 2017). This would explain the coexistence in the peri-Gondwanan record of upper Berounian endemic taxa with the Boda Event "immigrants" (*Nicolella* Fauna) as it has been documented in the Portixeddu Formation of Sardinia and in the Gabian Formation of the Montagne Noire (Colmenar, 2015 and references therein). These co-occurrences of typical upper Berounian taxa with the "immigrants" that have previously been considered exclusively Kralodvorian, makes establishing the location of the Berounian-Kralodvorian boundary in high-latitude peri-Gondwana very difficult. The upper boundary of the Kralodvorian with the Hirnantian is, however, recognisable either by the presence of glaciogenic sediments or by the presence of the *Hirnantia* Fauna itself.

Furthermore, in high-latitude peri-Gondwanan fossil record, the general scarcity of graptolites and conodonts and the largely endemic nature of the shelly faunas, add difficulties for correlating the successions in this region with the global chronostratigraphy (Gutiérrez-Marco *et al.* 2015). The correlation for the Kralodvorian Regional Stage with the international scale can be attempted only when the conodont *Amorphognathus ordovicicus* (the FAD of which marks the beginning of the upper Katian, Ka3 stage slice; Bergström *et al.* 2009) is recognizable, requiring the development of appropriate litho- and biofacies, potentially distant from its FAD (Gutiérrez-Marco *et al.* 2015). In addition, the absence of the graptolite *Dicellograptus complanatus* in peri-Gondwana (excepting for few isolated and stratigraphically unclear occurrences in France; Gutiérrez-Marco *et al.* 2015), the appearance of which characterizes the Ka4 stage slice (Bergström *et al.* 2009), makes correlation with the uppermost Katian problematic.

In Morocco, due to the absence of suitable conditions for the settlement of the *Nicolella* Fauna (Colmenar 2015) and the very shallow onshore shelf facies (Gutiérrez-Marco *et al.* 2017) that prevent the occurrence in that region of the deep water *Foliomena* Fauna, the Kralodvorian is marked by the presence of the *Mucronaspis termieri-Flexicalymene ouzregui* assemblage (Gutiérrez-Marco *et al.* 2017).

Proposal for the subdivision of the Kralodvorian Regional Stage

Herein we propose a subdivision of the Kralodvorian Regional Stage based on brachiopod occurrences, which allows an even more precise correlation within western peri-Gondwana. The division of the Kralodvorian into a lower and upper part must take into consideration that the occurrence of brachiopod assemblages is usually facies controlled. For this reason, we propose both deep- and shallow-water brachiopod markers, which are widespread throughout the main high-latitude peri-Gondwana localities and sections (Fig. 8). In addition, it is important to note that it would be necessary to complement this proposed subdivision with the stratigraphic ranges and occurrences of other fossil groups such as graptolites, conodonts and chitinozoans, among others.

Deep-water facies. – The *Foliomena* Fauna (Harper 1979) is known from lower-mid Katian deep-water facies of low-mid latitude settings (Rong *et al.* 1999 and references therein), but at higher latitudes (peri-Gondwana) it is only known from the uppermost Kralodvorian. The first report of this fauna in high-latitude peri-Gondwana came from the "Perník Bed" of the upper part of the Králův Dvůr Formation (Havlíček & Mergl 1982), which, as discussed above, represents the uppermost Kralodvorian in the Barrandian area. The *Foliomena* Fauna was also described from the "Cyclopygid Bed" of the Punta S'Argiola Member of the Domusnovas Formation of Sardinia (Villas *et al.* 2002a), approximately 35 m above the Sardic FAD of *Amorphognatus ordovicicus,* and about 18–20 m below the conformably overlying Hirnantian Rio San Marco Formation (Leone *et al.* 1991, Villas *et al.* 2002a). The *Foliomena* Fauna was recently identified in the uppermost Porto de Santa Anna Formation (Colmenar *et al.* 2016) in approximately coeval but deeper facies than those containing the fauna described in this paper (which includes a few minute, and perhaps transported, brachiopods such as *Jezercia* – see above – from the *Foliomena* Fauna).

Based on the records from Bohemia, Iberia and Sardinia, the occurrences of the *Foliomena* Fauna in high-latitude peri-Gondwana seems to be restricted to the uppermost Kralodvorian. This is probably due to the fact that the deep marine conditions required for the settlement of this fauna only occurred in this realm during the late Kralodvorian, possibly related to the transgression linked to the Boda Event.

Here we propose to use the records of the *Foliomena* Fauna as an indicator of the upper Kralodvorian. In addition, the presence in Bohemia of brachiopods of the *Rafanoglossa* Community could be indicative of the lower Kralodvorian in the Bohemian area. However, the co-occurrence of *Rafanoglossa* with *Foliomena folium* at the Levín section (M. Mergl personal communication) has to be investigated in other areas that, until now such co-occurrence has not been registered. In the same way, the use of this community as a marker of the lower Kralodvorian in deep water facies development of peri-Gondwanan regions must be subject to findings or more thorough studies of this community outside Bohemia).

Shallow-water facies. – The brachiopod taxa *Porambonites* and *Kjaerina* (*Villasina*) are found in shallower facies and they are represented by species that have different stratigraphical ranges within the Kralodvorian. The biostratigraphical distribution of these brachiopods could therefore provide additional criteria for subdivision of the stage. Only two species of *Porambonites* are known in the Kralodvorian of high-latitude peri-Gondwana – *Porambonites magnus* (Meneghini, 1980), originally described from Sardinia and *Porambonites dreyfussi* Havlíček, 1981, from the Montagne Noire. *Porambonites dreyfussi* has been found always above *P. magnus* in the Kralodvorian (Havlíček 1981) Gabian Formation (Colmenar *et al*. 2013). This pattern is also observed in the Portuguese Kralodvorian sequences (this paper). *Porambonites dreyfussi* always occurs in the Riba de Cima Member of the Ferradosa Formation (Kralodvorian) whereas *P. magnus* is restricted to the lower part of the Porto de Santa Anna Formation (uppermost Berounian to lower Kralodvorian) and to the Poiares Member (uppermost Berounian to lower Kralodvorian), lower member of the Ferradosa Formation (Young 1985, Colmenar 2015).

Currently, *Kjaerina* (*Villasina*) includes four species. Among them, *Kjaerina* (*V.*) *meloui* (Colmenar, 2016), from the Rosan Formation of the Armorican Massif is exclusively Kralodvorian. On the other hand, *Kjaerina* (*V.*) *almadenensis* (Villas, 1995) from the Spanish Central Iberian Zone ranges from the uppermost Berounian to the Kralodvorian. In the Rosan Formation *Kjaerina* (*V.*) *meloui* has only been recorded from above the levels of occurrence of *Kjaerina* (*V.*) *almadenensis* within the Rosan Formation (Colmenar 2016). This situation was also observed in Portugal (this paper) where *Kjaerina* (*V.*) *meloui* is restricted to the Riba de Cima Member of the Ferradosa Formation and *Kjaerina* (*V.*) *almadenensis* to the lower part of the Porto de Santa Anna Formation and to the Poiares Member.

These criteria suggest that, in areas where the deep water facies containing the *Foliomena* Fauna is absent, the presence in shallow facies of either of the brachiopod species *Porambonites dreyfussi* or *Kjaerina* (*Villasina*) *meloui* may indicate an upper Kralodvorian age, whereas the presence of *Porambonites magnus* and/or *Kjaerina* (*V.*) *almadenensis* could be diagnostic of the lower Kralodvorian.

Conclusions

The study of Kralodvorian brachiopod-dominated associations from rocks of the Portuguese Central Iberian Zone, together with a comparison of other benthic associations from the main Ordovician successions of peri-Gondwana, has allowed redefining the base and top of the Kralodvorian Regional Stage. The proposed informal subdivision of this stage, based on shallow- and deep-water brachiopod occurrences, may be complemented by further investigation, in these key successions, of other biostratigraphically relevant fossil groups such as graptolites, conodonts and chitinozoans.

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