

Geological Society, London, Special Publications

The 'microcontinent' Perunica: status and story 15 years after conception

Oldrich Fatka and Michal Mergl

Geological Society, London, Special Publications 2009; v. 325; p. 65-101
doi:10.1144/SP325.4

Email alerting service

[click here](#) to receive free email alerts when new articles cite this article

Permission request

[click here](#) to seek permission to re-use all or part of this article

Subscribe

[click here](#) to subscribe to Geological Society, London, Special Publications or the Lyell Collection

Notes

Downloaded by on 16 December 2009

The 'microcontinent' Perunica: status and story 15 years after conception

OLDŘICH FATKA^{1*} & MICHAL MERGL²

¹*Institute of Geology and Palaeontology, Faculty of Science, Charles University, Albertov 6, Prague 2, 128 43, Czech Republic*

²*Department of Biology, University of West Bohemia, Klatovská 51, 306 19, Plzeň, Czech Republic*

**Corresponding author (e-mail: fatka@natur.cuni.cz)*

Abstract: Central Europe consists of a complex mosaic of more or less independent terranes with varying tectonometamorphic histories, usually also of different lithological compositions and protolith, and thus it is reasonable to suppose that the majority of these blocks have experienced somewhat different palaeogeographical evolution. The present terrane juxtaposition has been interpreted in general as a result of the Variscan collision of peri-Gondwanan and peri-Baltic derived terranes, with Gondwana on one side and Baltica and/or Laurentia on the other side. However, reconstruction of the pre-Variscan development and mutual palaeogeographical relationships remains a major challenge of interpretation.

In early Palaeozoic times there was only one supercontinent, Gondwana, and three other major continents, Laurentia, Baltica and Siberia (e.g. Cocks & Torsvik 2002). Numerous smaller but important terranes are supposed to have existed, grouped around the larger continents. The history of Baltica was elaborated in detail by Cocks & Torsvik (2005). The complicated picture of the numerous smaller terranes surrounding Siberia has also been reconstructed recently (Cocks & Torsvik 2007). Similar analyses have been published also for Europe (Cocks 2000, 2002; Cocks & Torsvik 2006) but the complicated geology of southwestern and Central Europe is still a matter of debate (e.g. Robardet 2003), mainly because the poorly defined terranes resulted from the tectonic instability of 'segments' incorporated into this area during three major orogenies, the Cadomian, Variscan and Alpine episodes.

For the Variscan orogeny, the decisive role of the Baltic Shield on one margin and Gondwanan Africa on the other side is generally accepted (Fortey & Cocks 2003; but see Landing 2005). However, reconstruction of post-Cadomian and pre-Variscan history of separate European segments is influenced strongly by the reality that both the Variscan and partly also the Alpine orogenies destroyed major parts of the former sedimentary basins, and importantly also altered their relative positions. Consequently, southwestern and central Europe is composed of more or less sharply truncated terranes. Numerous attempts to identify and characterize separate terranes within the Variscan belt, including the Bohemian Massif, have been published (e.g. Franke

1989; Matte *et al.* 1990; Bachtadse *et al.* 1995; Tait *et al.* 1997; Pharaoh 1999; Matte 2001; Winchester *et al.* 2002; Vecoli & Le Hérisse 2004).

In the past 30 years the evaluation of palaeomagnetic data and fossil associations has provided a possibility to establish similarities and differences on a regional scale. Such studies have resulted in the separation and general acceptance of several palaeogeographical domains within Europe, namely, Baltica, peri-Baltica, peri-Gondwana with Avalonia, Armorica and more recently also Perunica, Iberia, and/or an Armorican terrane assemblage (ATA).

Armorica and Avalonia

Armorica was defined originally by Van der Voo (1979) on the basis of palaeomagnetic data. According to that definition it embraced most of western Europe, including southwestern Britain and Wales, various sectors of Variscan Europe south of the British Isles, part of northern Africa, and probably also the Avalon Peninsula of Newfoundland and New England of North America. Since this original definition, the geographical extent of Armorica has undergone several restrictions and redefinitions, resulting in a general reduction of its extent. The first major change was the distinction of Avalonia, which was based first on palaeontological arguments (Cocks & Fortey 1982, 1990), and was supported later by palaeomagnetic data (e.g. Bachtadse *et al.* 1995). Avalonia is geologically well defined, being separated by the two closed Caledonian sutures: the Iapetus Ocean suture separating Avalonia from

North America, and the Tornquist Ocean suture, part of the Trans-European Suture Zone, marking the boundary with Baltica. The younger Variscan Rheic Ocean suture separates Avalonia from Gondwana to the south. The boundaries of Avalonia were revised and described in detail by Cocks *et al.* (1997), and Avalonia thus now includes a North American sector embracing southern parts of eastern Newfoundland (Avalon), most of the Maritime Provinces of Canada and the eastern US seaboard as far as Cape Cod, Massachusetts, and perhaps southern Carolina, and a European sector with southern Ireland, Wales, England, Belgium, the Netherlands and parts of northern Germany, and most probably also northwestern Poland (Pomerania; Cocks *et al.* 1997; Urung *et al.* 1999; Vecoli & Samuelsson 2001; Cocks 2002).

The well-established early Ordovician separation of Avalonia, and its drift across the narrowing Iapetus Ocean associated with opening of the Rheic Ocean to the south, was proposed originally on the basis of palaeontological information (Cocks & Fortey 1982). This scenario has been supported by palaeontologists (e.g. Fortey & Cocks 2003, and references therein) and also by palaeomagnetic studies (e.g. Torsvik *et al.* 1993).

Armorican terrane assemblage and Cadomia

Increasing palaeontological and palaeomagnetic data provided a possibility to evaluate regional as well as local differences in greater detail. This resulted in continual redefinition of the boundaries of separate terranes (Cocks *et al.* 1997; Servais & Fatka 1997; Cocks & Fortey 1998; Moczydlowska 1999; Urung *et al.* 1999). One of most important changes has been the proposal of an Armorican terrane assemblage (ATA) by Tait *et al.* (1994, 1997) and Franke (2000). Originally the ATA included Franconia, Saxothuringia and Bohemia; later Schätz *et al.* (2002) incorporated the Saxothuringian terrane, Teplá–Barrandian region, and Iberian and Armorican massifs. The same terranes were incorporated also in the ‘Iberian–Armorican Terrane Collage’ of Linnemann & Romer (2002) (Iberia, Armorica, Saxothuringia). Recently, Cocks & Torsvik (2006) incorporated only the Iberian Peninsula and most of France, and separated Perunica from the ATA.

A different approach to distinguishing terranes has been applied by petrologists analysing the age of basements of terranes. In general, the ATA is synonymous with Cadomia, defined as peri-Gondwanan terranes with basement about 2 Ga old. Keppie *et al.* (2003) incorporated the Ossa–Morena and Central Iberian zones of Spain, the French Armorican massif and the Massif Central, and questionably also the Saxothuringian and

Moldanubian zones of Germany and the Czech Republic, respectively.

Perunica and its definition

The first attempts to evaluate the history of the Ordovician fauna of the Teplá–Barrandian region, at that time on the basis of only provisional Early Palaeozoic palaeogeography, were published by Havlíček (1976, 1982). However, the earlier establishment of an alternative regional chronostratigraphical scheme by Havlíček & Marek (1973) incorporated an expression of major faunal differences. On the basis of benthic brachiopods, Havlíček & Marek (1973) defined four new stages, Dobrotivá, Beroun, Králodvov and Kosov, for the Middle and Upper Ordovician; thus the paper defining the original concept of the microcontinent Perunica published by Havlíček *et al.* (1994) is essentially only a palaeogeographical expression of the earlier established faunal differences. Havlíček *et al.* (1994) brought together a major part of the Bohemian Massif, involving the Moldanubian, Barrandian and Saxothuringian (Saxothuringian–Lugian) zones, which constituted a separate microplate during the Early Palaeozoic, and for palaeogeographical purposes named it Perunica.

In the last 15 years, some workers have continued to use names such as Bohemia (e.g. Tait *et al.* 1994) or Teplá–Barrandian (e.g. Schätz *et al.* 2002), or even the questionable Barrandian Basin, but the palaeogeographical designation of Perunica has been cited in more than 60 papers dealing with various aspects of palaeontology, stratigraphy or palaeogeography. Numerous new data have been published since the original paper was published, and it now seems appropriate to revise the original definition of Perunica and to bring it in agreement with more recent data.

Paleontology. A majority of papers have focused on systematics and palaeogeography of Ordovician and Silurian trilobites, brachiopods, bivalves and cephalopods. Perunica is employed as a useful designation for a peri-Gondwanan area of species development (for a summary, see Fortey & Cocks 2003).

Palaeomagnetic data. Critical and comprehensive summaries of the earlier palaeomagnetic data from the Teplá–Barrandian region were published by Torsvik *et al.* (1990), and were supplemented, discussed and reinterpreted recently by Nysaether *et al.* (2002).

The aim of this contribution is to provide a comprehensive review of available palaeontological data on Neoproterozoic, Cambrian and Ordovician fossils of the Teplá–Barrandian region, complemented by brief remarks on Silurian and Devonian

faunas, with the aim of discussing the applicability of existing palaeomagnetic, sedimentological and palaeontological data for reconstruction of the palaeogeographical history of this region.

Teplá–Barrandian region within the Bohemian Massif

The largest exposed area of the Variscan orogen in Central Europe is represented by the Bohemian Massif, which forms a major part of the Czech Republic and adjacent areas in Austria, Germany and Poland (Fig. 1). The Bohemian Massif encompasses three main units in which palaeontologically and geochronologically well-dated Proterozoic to Devonian sequences are present (Fig. 2): (1) Bohemikum, with four main regions: the Teplá–Barrandian region, Železné hory area and Hlinsko Zone, metamorphic islands within the Central Bohemian Granitic Pluton, and the Rožmitál region; (2) the Krkonoše–Jizera Unit; (3) Moravosilesicum, including the Moravian Karst, Velké Vrbno Unit and Drahany Upland. In addition, about 10 geographically very restricted occurrences of palaeontologically dated outcrops of Lower Palaeozoic rocks have been established in various regions of the Bohemian Massif (Fig. 2).

The Teplá–Barrandian region in West Bohemia together with eastern Bavaria and Thuringia represents one of the easternmost segments of the Avalonian–Cadomian tectonostratigraphical belt, which was consolidated between 670 and 550 Ma and was not affected by high-temperature–low-pressure metamorphism during the Variscan orogeny. The basement of these units, if known, is composed of late Proterozoic sediments, including the late Proterozoic flysch and volcanites typical of an arc-related setting. Most of the basement rocks of the region underwent very low-grade to amphibolite-facies metamorphism and deformation at about 550–540 Ma (Zulauf 1997; Zulauf *et al.* 1999). In contrast to other units of the Bohemian Massif, the thickened Cadomian crust collapsed in the Neoproterozoic and allowed deposition of thick sequences of continental clastic deposits in several graben structures; for example, the Příbram–Jince and Skryje–Týřovice basins of the Barrandian area or in the Franconian Forest in Germany. The general evolution of the sequence of sedimentary and volcanic rocks reflects subsidence associated with extension in an intracontinental to passive marginal setting.

Neoproterozoic

Several thousand metres of marine clastic deposits volcanites accumulated in a rapidly subsiding

marginal sea bordering the margin of Gondwana, positioned most probably on oceanic crust. The sequence is composed of siliciclastic terrigenous rocks dominated by greywackes, siltstones and shales. Recently two major lithostratigraphical units have been distinguished, the Kralupy–Zbraslav and the Štěchovice groups. A rather monotonous complex of turbidites (greywackes, siltstones) with silicites, volcanites and black shales characterizes the extensive exposures of the Kralupy–Zbraslav Group in Central and West Bohemia (Cháb & Pelc 1973; Cháb 1978).

The volcanites belong to three main series of alkaline, transitional and tholeiitic geochemistry, corresponding to volcanic arc and back-arc geotectonic settings (Dörr *et al.* 2002). Neoproterozoic volcano-sedimentary successions belong to an active island arc and sedimentation represents deposition in a back-arc basin until at least 570 Ma. A change in the geotectonic regime from convergence to transtension is indicated by a strong increase in heat flow at around 545 Ma, associated with an angular unconformity between Cadomian basement and Lower Paleozoic sequences near the Precambrian–Cambrian boundary.

Analyses of lithological development of Neoproterozoic rocks support their peri-Gondwanan origin but do not provide any reliable information for more precise palaeogeographical positioning. Fossils are represented solely by organic-walled microfossils, which allow correlation of both groups with the Brioverian of the Armorican Massif and confirm a Late Rhiphaean to Vendian age (Konzalová 1981; Fatka & Gabriel 1991). However, they do not provide any possibility for palaeogeographical interpretation. The absence of palaeomagnetic data excludes reliable positioning of the Teplá–Barrandian region at this time.

However, analyses of the palaeontological content of the 'lower' Cambrian Paseky Shale and 'middle' Cambrian Jince Formation combined with palaeomagnetic data offer much better datasets for interpretation of possible positioning of the Teplá–Barrandian region during the Cambrian. Such analyses are biased by various factors, but recent evaluation of echinoderm, trilobite and brachiopod assemblages provides a reliable picture of their distribution within the inshore–offshore transect, which could be well used to restore the palaeogeographical position of this area during the Cambrian.

Cambrian

Within the Teplá–Barrandian region, Cambrian rocks are known from three separate areas: the larger and more complete Příbram–Jince Basin, the Skryje–Týřovice Basin and the Železné hory area (Figs 2 & 3). Stratigraphical subdivision of

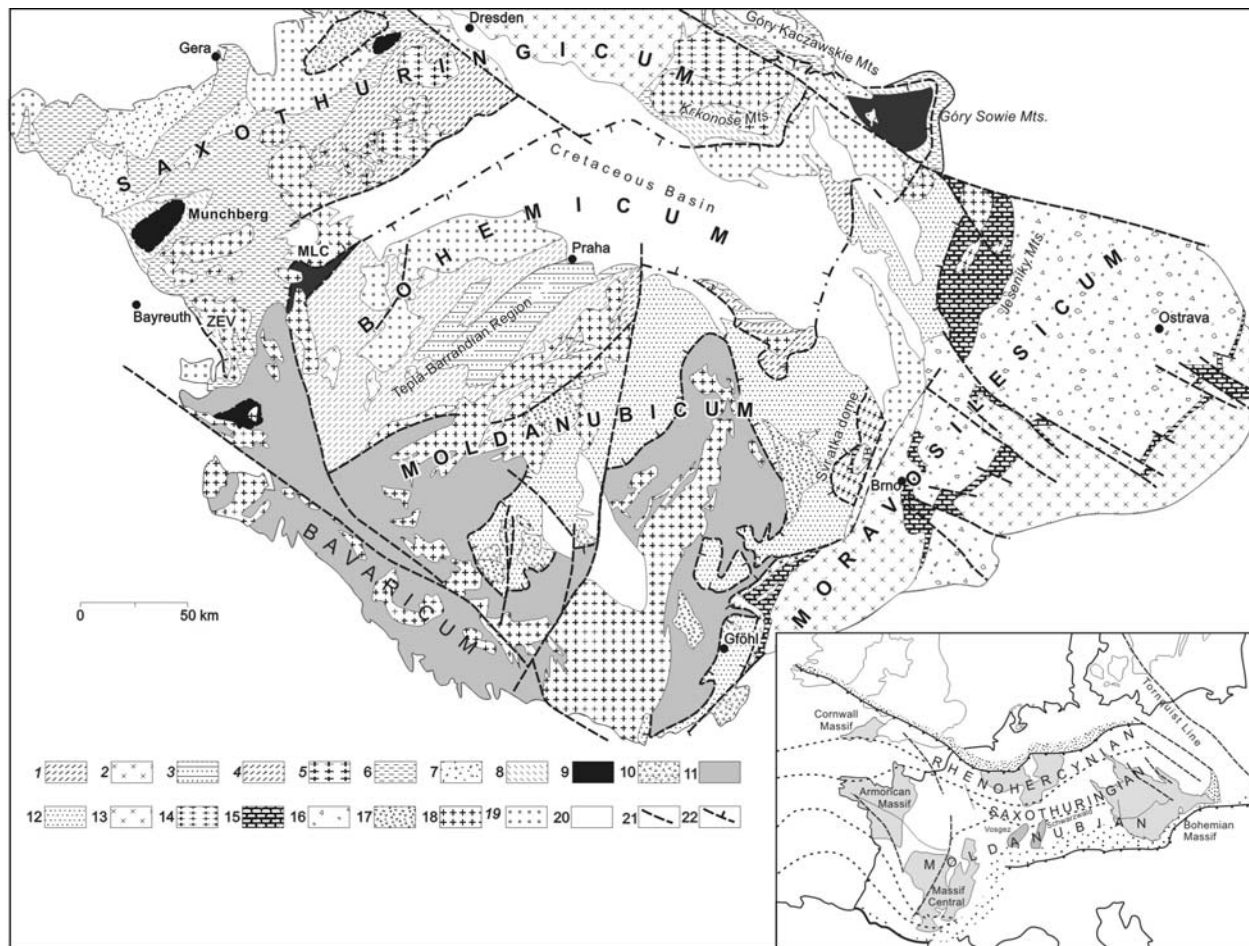


Fig. 1. Continued.

Cambrian rocks has been summarized by Havlíček (1971a), Chlupáč *et al.* (1998) and Chlupáč (1999a).

Příbram–Jince Basin. The Neoproterozoic succession is overlain unconformably by a c. 2500 m thick sequence of coarse-grained clastic deposits (conglomerates and sandstones with interlayers of greywackes to shales of the Hluboš–Žitce to Chumava–Baština formations) passing upwards into greywackes and shales of the Jince Formation and then into volcanites. The stratigraphical subdivision, involving a repetition of comparatively fine- and coarse-grained lithotypes, makes it possible to distinguish 13 lithostratigraphical units (Havlíček 1971a), grouped into eight formations (Fig. 4). Fossils occur in two levels, in the 'lower' Cambrian Paseky Shale Member of the Holšiny–Hořice Formation, and in the 'middle' Cambrian Jince Formation (Fig. 4).

The Paseky Shale Member. The first reported fossil, the enigmatic aglaspid merostome *Kodymirus vagans* Chlupáč & Havlíček (1965), was described at a time when the Paseky Shale Member was assumed to represent a marginal facies of the younger Jince Formation. The true stratigraphical position of the Paseky Shale, some 800–1500 m below the Jince Formation, was later determined by Havlíček (1968). Investigations at five fossiliferous localities (Chlupáč *et al.* 1996) resulted in an integrated study of various fossil groups and lithology (Kukal 1996). Based on results of these studies, this early Cambrian biota was dominated by the very distinct *Kodymirus*. Association characterized by three genera of non-trilobite arthropods (*Kodymirus*, *Kockurus* and *Vladicaris*; see Chlupáč 1995) associated with diversified trace fossils (?*Rusophycus*, *Monomorphichnus*, *Diplichnites*, *Dimorphichnus* and ?*Bergaueria*; see Mikuláš 1996), macroscopic algae (*Marpolia* Walcott 1919; see Steiner & Fatka 1996), organic-walled microfossils (filamentous microfossils *Rectia* Jankauskas 1989;

Palaeolyngbya Schopf 1968; *Botuobia* Pjatiletov 1979; *Siphonophycus* spp. and *Polythrachoides* Hermann 1974 emend. Hermann 1976 in Timofeev *et al.* 1976; prasinophyte and acritarch genera *Retisphaeridium* Staplin, Jansonius & Pocock 1965; *Skiagia* Downie 1982, *Adara* Fombella 1977; *Sinia-nella* Yin 1980 emend. Zang in Zang & Walter 1992; *Leiosphaeridia* spp. and microscopic resting traces, e.g. *Ceratophyton vernicosum* Kirjanov, 1979 in Volkova *et al.* 1979, see Fatka & Konzalová 1996). The distribution of all the taxa recognized from the most fossiliferous locality at Kočka has been summarized by Fatka *et al.* (2004).

The noticeable absence of groups typical of the Sepkoski Cambrian Fauna such as trilobites, echinoderms and brachiopods, combined with the presence of spectacular arthropods and the scarcity of process-bearing acritarchs in the microfossil assemblage, reflects a marginal environment; that is, the biota reflects restricted marine conditions (Fig. 5).

The *Kodymirus* Association inhabited shallow subtidal plains characterized by greywackes to fine shales. Precise dating within the 'early' Cambrian is difficult because of the absence of stratigraphically important taxa. Fatka & Konzalová (1996) reported a rich assemblage of organic-walled microfossils dominated by filamentous cyanobacteria, spherical leiospherids and rare acritarchs, including the occurrence of ?*Volkovia*, which could date the Paseky Shale Member within the *Volkovia–Liepaina* Zone of Moczydlowska (1999); that is, late in the as yet unnamed series of the Cambrian.

The Jince Formation. This unit in the Příbram–Jince and Skryje–Týřovice basins includes the best preserved and most diverse Cambrian faunas in Central Europe, displaying environmentally controlled distribution of assemblages (Elicki *et al.* 2008).

The lower, thick sequence of clastic sediments (over 1500 m) underlying the Jince Formation characterizes the maximum subsidence in the Brdy

Fig. 1. Tectonic sketch map of the Bohemian Massif showing the main terranes (modified after Matte *et al.* 1990). Bohemium (Teplá–Barrandian Unit): 1, Late Proterozoic volcano-sedimentary sequences; 2, Pre-Variscan (Cadomian granitic rocks); 3, Early Palaeozoic metasediments and volcanic rocks (Cambrian to Devonian). Saxothuringicum: 4, Late Proterozoic metasediments; 5, Cadomian metagranitoids (orthogneisses); 6, Early Palaeozoic metasediments (Cambrian to Devonian); 7, Early Carboniferous diastrophic sediments. Autochthonous units (in Saxothuringicum and Moldanubicum): 8, lower part of allochthonous units consisting of weakly metamorphosed metasediments, basic volcanic rocks and ultrabasic rocks, 9, high-grade rocks (gneisses, metagabbros, eclogites); 10, granulite massifs including eclogites and HP mantle peridotites. Moldanubicum: 11, high-grade gneisses, probably Late Proterozoic to Early Palaeozoic in age (Ostrong and Drosendorf groups); 12, allochthonous complexes of the Gföhl Unit with relics of HP rocks. Moravosilesicum (including Brunovistulicum): 13, Cadomian basement of the Brunovistulicum (Cadomian granitic rocks and their metamorphic mantle); 14, Cadomian orthogneisses of the Moravosilesian Units; 15, Early to Late Palaeozoic volcano-sedimentary sequences of the Moravosilesicum (including basement units); 16, Viséan to Namurian diastrophic sediments (Culm facies) in the upper part with transition to weakly deformed sediments of the Variscan foredeep. Variscan granitoids: 17, melanocratic granites and syenites (durbachites); 18, tonalites to granites; 19, Late Carboniferous to Permian clastic sediments and volcanic rocks (epi-Variscan platform sediments); 20, post-Permian cover; 21, major fault zones; 22, thrust, nappe boundaries. (Drawn by V. Kachlík.)

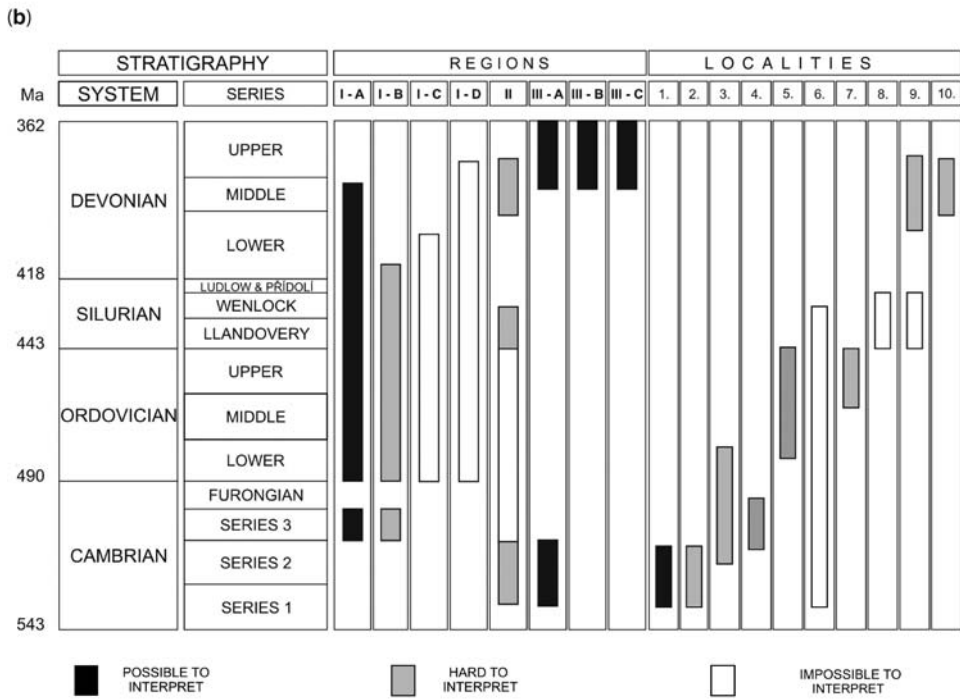
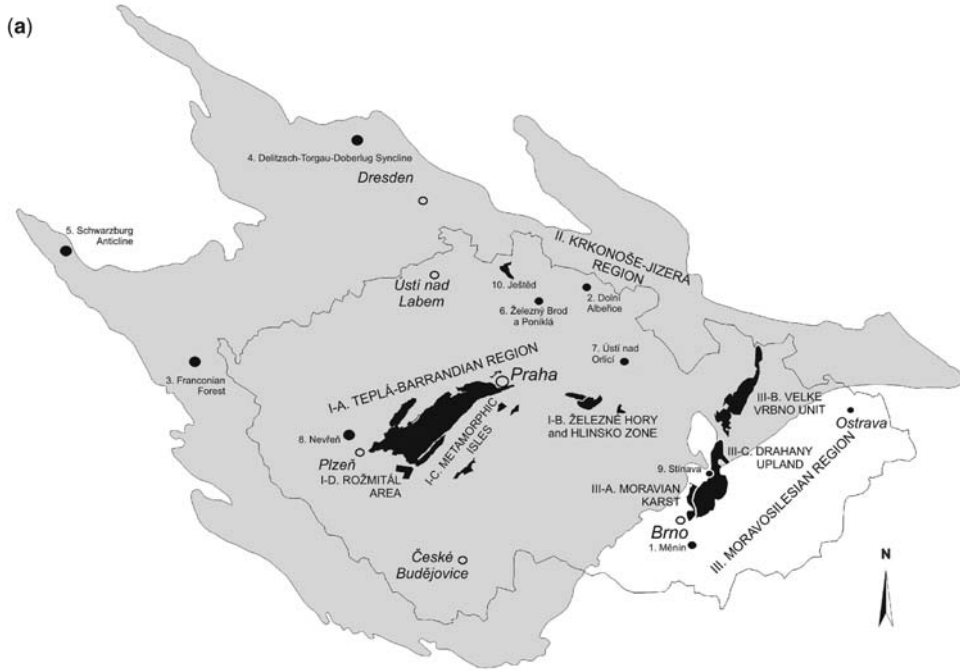


Fig. 2. (a) Map of Czech Republic showing regions and localities with Cambrian to Devonian fossils. (b) Potential of fossils for interpretation of palaeogeographical position.

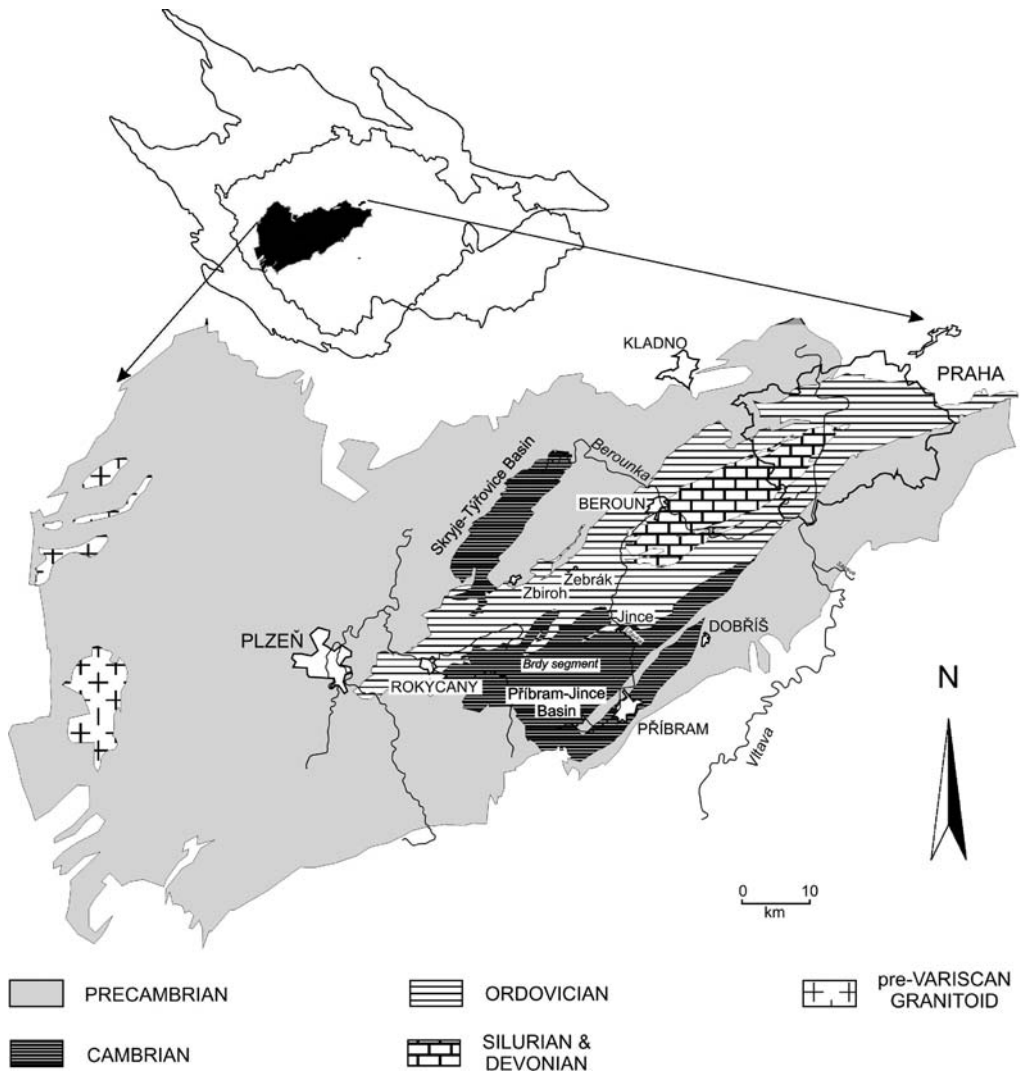


Fig. 3. Geology of the Teplá-Barrandian region with the Cambrian Příbram-Jince and Skryje-Týřovice basins and the Ordovician-Devonian Prague Basin.

area of the Příbram-Jince Basin. An important change in basin geometry is associated with the marine ingress, represented by the 100–450 m thick Jince Formation. At this time the main depocentre shifted eastwards to the Litavka river valley (Havlíček 1971a). Within the Jince sequence it is possible to distinguish at least two major facies areas in the basin: a shallower Brdy segment and the deeper-water Litavka valley segment (Fig. 3). For the deepest segment as preserved in the Litavka valley, several bathymetrically controlled associations have been characterized (Fatka 2000). The even distribution of fossil assemblages through the formation in this region is possibly explained

by a major transgressive-regressive cycle, with one or two fluctuations associated with pronounced changes in the depositional rate (Fatka 1990, 2000). Analyses of the Jince biota reveal a well-developed bathymetric differentiation. Shallow marine coarser-grained sediments (sandy greywackes and greywackes) are typified by the shallow-water *Lingulella* Biofacies at the base as well as at the top of the formation in the Litavka sequence (Fig. 6a). Slightly deeper-water greywackes to coarse shales are dominated by the Polymeroid Trilobite Biofacies (*Ellipsocephalus*, *Paradoxides*, *Conocoryphe*, *Ptychoparia*, *Acadolenus*, *Litavkaspis*). These two biofacies are predominant in the

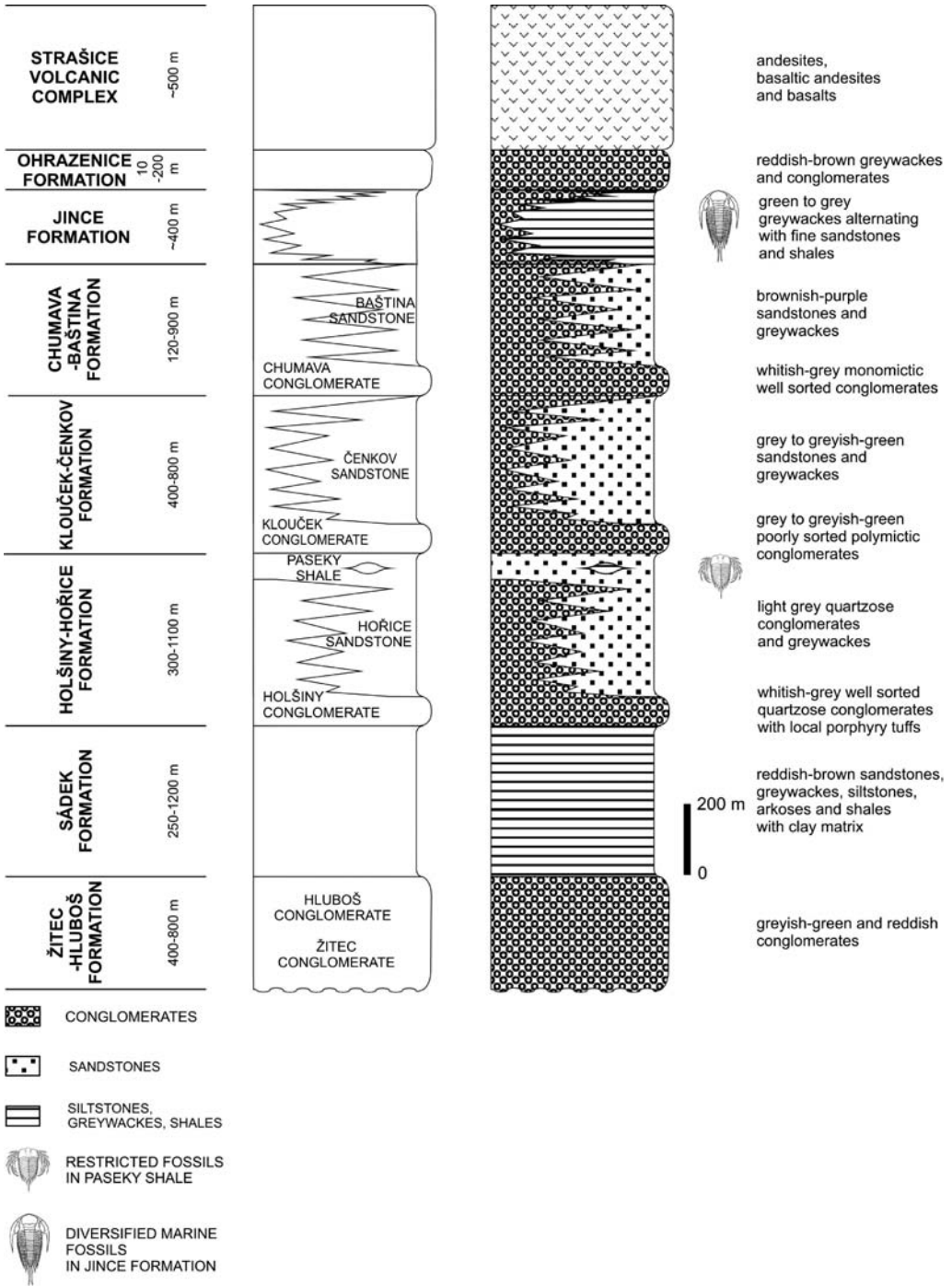


Fig. 4. Cambrian stratigraphy in the Příbram–Jince Basin (adopted after Havlíček 1971a; Elicki *et al.* 2008).

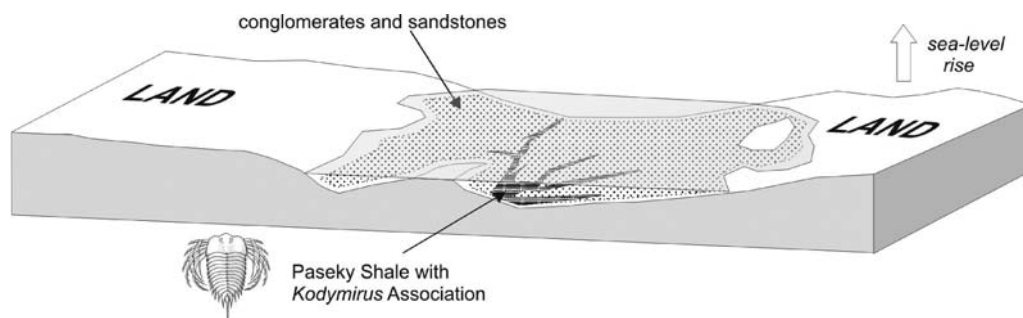


Fig. 5. Diagrammatic history of the Příbram–Jince Basin and the 'early' Cambrian Holšiny–Hořice Formation, with the *Kodymirus* Association in the Paseky Shale.

lower and upper thirds of the Jince Formation in this region, and in the complete thickness of the formation in the WNW area of the Příbram–Jince Basin; for example, in the Brdy segment (Fig. 6b).

Apart from the widely distributed *Paradoxides* and *Ellipsocephalus* and the endemic *Ptychoparia*, the other genera indicate a peri-Gondwanan origin. *Conocoryphe* is widely distributed in southwestern and Central Europe (various areas of Spain, Montagne Noire, Sardinia, Franconian Forest, Skryje–Týřovice Basin and Železné hory area) and Turkey. A typical 'Mediterranean' species is the trilobite *Acadolenus*, as is the cinctan echinoderm *Asturicystis*, which has been reported from the West Asturian–Leonese zone of Spain. The seemingly endemic genus *Litavkaspis* was reported from a similar stratigraphic level in slightly metamorphosed sediments of the Carolina terrane.

In the Litavka valley, the middle part of the formation, comprising mudstones with fine greywackes, is characterized by a dominance of agnostid trilobites of the miomerid Biofacies (Fig. 6c). Three associations can be identified within the transgressive sequence; namely, the relatively shallower *Peronopsis*–*Phalagnostus* Association, the deeper *Phalacroma*–*Condylopyge* Association, and the deepest *Onymagnostus*–*Hypagnostus* Association (Fatka *et al.* 2007).

The *Peronopsis*–*Phalagnostus* Association contains only the eponymous agnostid genera, associated with common polymeroids of the genera *Ellipsocephalus*, *Ptychoparioides*, *Acadolenus*, *Litavkaspis*, *Ptychoparia* and *Solenopleurina*. In the *Phalacroma*–*Condylopyge* Association, the eodiscoid *Dawsonia* and the agnostoid *Pleuroctenium* also occur rarely, associated with the common polymeroid genera *Paradoxides* (*Hydrocephalus*), *P. (Eccaparadoxides)*, and *P. (Acadaparadoxides)*. *Ptychoparioides*, *Ptychoparia*, *Ellipsocephalus*, *Solenopleurina* and *Conocoryphe* also occur, but more rarely. The *Onymagnostus*–*Hypagnostus* Association incorporates the locally

abundant genera *Onymagnostus*, *Hypagnostus*, *Tomagnostus* and *Doryagnostus*. *Peronopsis* and *Phalagnostus* as well as paradoxid trilobites (*Paradoxides* and its subgenera *Paradoxides*, *Eccaparadoxides*, *Acadaparadoxides*, *Hydrocephalus*). The blind genus *Conocoryphe* and the large bivalve arthropod *Tuzoia* can be present in all three associations. All three miomerid associations are developed only in the Litavka valley; the first association is present also in the central, more western part of the basin, but agnostids are absent in the westernmost sectors of the basin (e.g. in the Brdy segment).

The five cosmopolitan agnostid genera show an unusual pattern of distribution. *Peronopsis* is known world-wide, including southwestern Europe. *Onymagnostus*, *Hypagnostus*, *Doryagnostus* and *Tomagnostus* are known from Baltica but are completely absent from Spain, France, Germany and Turkey, whereas *Condylopyge* is present in Spain and Germany as well as in Britain, Newfoundland and Baltica. *Pleuroctenium* and *Phalagnostus* occur in Germany (Franconian Forest) and Britain, but are absent in southwestern Europe.

At least five substrate and bathymetrically related echinoderm associations can be differentiated in the Příbram–Jince Basin: shallow-water, more or less monospecific *Ceratocystis*, *Asturicystis* and *Stromatocystites* associations, all confined to well-aerated sandy to greywacke, rarely even muddy bottoms, whereas the *Lichenoides*–*Akadoocrinus* and *Etoctenocystis* associations (usually with more or less common eocrinoids *Acanthocystites*, *Vyscystis* and *Felbocrinus*) preferred more quiet, deeper conditions characterized by very fine sandy to muddy sedimentation (Fig. 6d). Echinoderm associations have been observed only in the Litavka river valley.

Ceratocystis has been reported in the Montagne Noire (France) and Baltica, and is most probably present also in the Franconian Forest of Germany. Ctenocystid and cinctan echinoderms appeared in Spain, France, and both the Příbram–Jince and

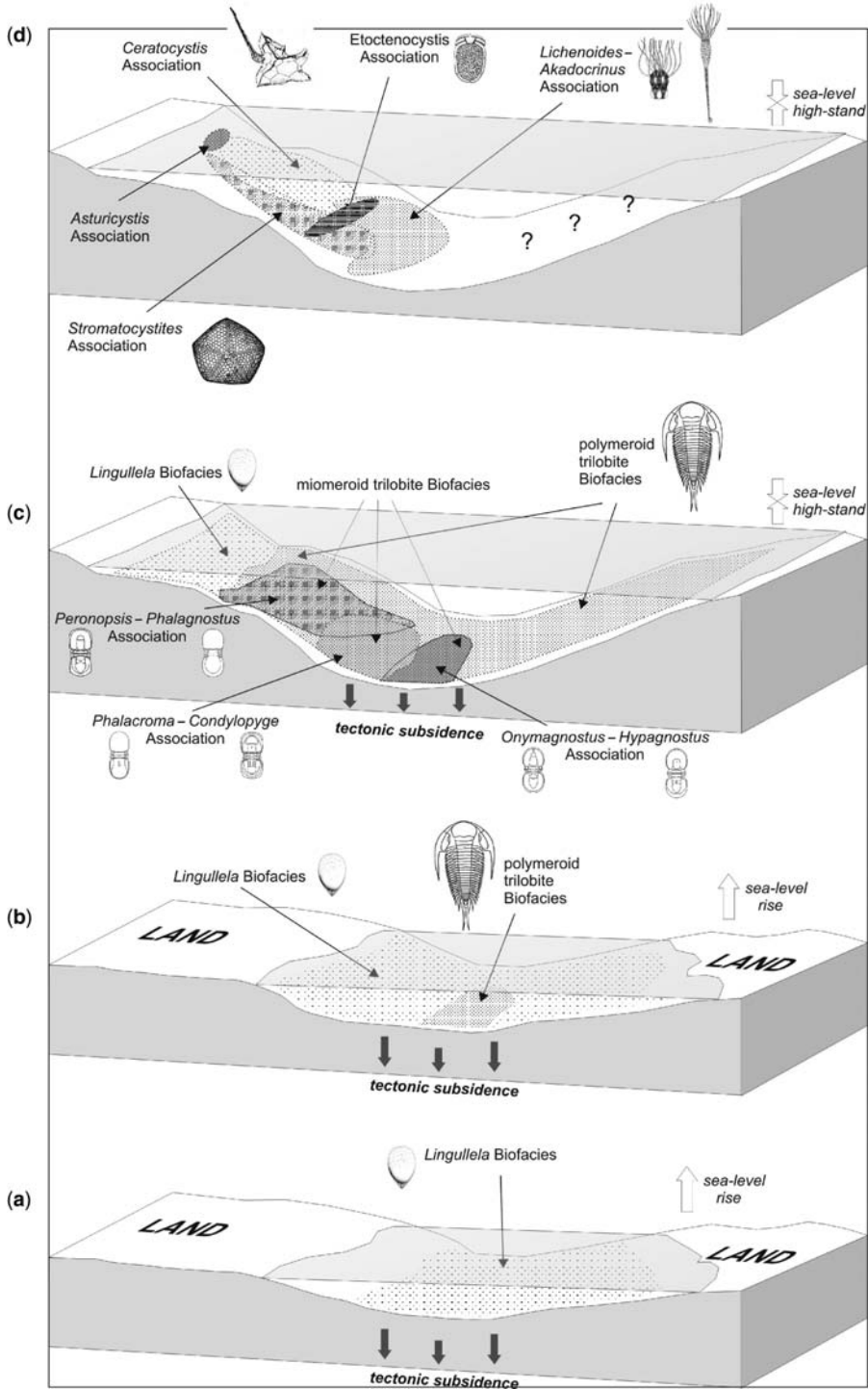


Fig. 6. Diagrammatic history of the Příbram–Jince Basin and its faunal associations in the Jince Formation. Only the left (WNW) slope of the basin is mostly illustrated, for simplification. Palaeoecological terminology is adopted from Fatka *et al.* (2006, 2007). **(a)** Beginning of marine incursion near the base of Jince Formation with the onset of

Skryje–Týřovice basins, as well as in Britain. Cinctans have also been reported recently from Italy (Sardinia) and Siberia, and ctenocystids are known also in Poland (Holy Cross Mountains), Laurentia and Australia (see below). *Stromatocystites* has been established in both the Přebram–Jince and Skryje–Týřovice basins and also in Newfoundland, Baltica and Australia. The eocrinoid genera *Lichenoides*, *Akadocrinus*, *Acanthocystites* and *Felbocrinus* are endemic forms.

The only eodiscid trilobite in the Teplá–Barrandian region, *Dawsonia bohémica*, has been identified recently in two other areas of SW Europe, namely in Sardinia (Elicki & Pilolla 2004) and in the Montagne Noire (Álvaro & Vizcaíno 2000). The cornute echinoderm genus *Ceratocystis* has a similar distribution, whereas the blind polymeroid *Ctenocephalus* cf. *coronatus* is known only from Italy (Sardinia, Cabitza Formation) and the Skryje–Týřovice Basin.

The rich acritarch assemblage of the Jince Formation does not provide any decisive palaeogeographical information (Vavřdová 1974a, b, 1982; Fatka 1989).

The Skryje–Týřovice Basin

A c. 200 m thick succession of Jince Formation in this region (conglomerates, sandstones, greywackes and shales) contains 'middle' Cambrian fossil assemblages (Fig. 7). The Cambrian sequence overlies the Neoproterozoic Kralupy–Zbraslav Group unconformably.

The basal monomict, white to grey Mileč Conglomerate and Sandstone, up to 10 m thick, contain generally fragmentary preserved brachiopods (*Pompeckium*; Havlíček 1970), locally common helcionelloid molluscs (*Helcionella*; Smetana 1918), and polymeroid trilobites (*Perneraspis*, *Germanopyge*,

Ptychoparioides and rarely *Paradoxides*; Šnajdr 1958) of the *Pompeckium*–*Germanopyge* Association (Fig. 8a). Kukal (1971) interpreted the high-energy succession as beach coastal barriers and bars, locally with very common brachiopods, the so-called 'Orthis' sandstone facies.

The Mileč Member is usually overlain by generally darker polymict conglomerates and greyish green greywackes to shales of the Týřovice Greywacke and Conglomerate, commonly containing pebbles of Proterozoic shales and greywackes. More or less fragmentary shells of locally common articulate brachiopods (*Pompeckium* and/or *Jamesella*), helcionelloid molluscs (*Helcionella*) and in some levels spectacular graptoloids and the lightly sclerotized *Wiwaxia* cf. *corrugata* (Matthew) occur (Maletz *et al.* 2005; Fatka *et al.* 2009). Up to 200 m of thick clayey shales and greywackes of the Skryje Shale (including silty and sandy intercalations) are the most widespread lithofacies, containing diverse faunas. The polymeroid trilobite Biofacies [with locally common genera *Conocoryphe*, *Ctenocephalus*, *Luhops*, *Paradoxides* (*Eccaparadoxides*), *P.* (*Hydrocephalus*), *Ptychoparia*, *Sao*, *Agraulos*, *Skreiaspis*, *Jincella*, *Ellipsocephalus* and the rare bivalved arthropod *Tuzoia*] is usually associated with the *Peronopsis*–*Phalagnostus* Association (Fig. 8a). In higher stratigraphic levels there are locally miomeroid trilobites of the *Phalacroma*–*Condylopyge* Association, with common *Pleuroctenium*, *Diplorrhina* and *Skryjagnostus*. Early ontogenetic stages of both miomeroid and polymeroid trilobites [e.g. *Sao* and *Paradoxides* (*Eccaparadoxides*)] are dominant, associated with rare brachiopods (*Bohemiella romingeri*) and cinctan, ctenocystoid and eocrinoid echinoderms (Fig. 8a).

Some lenses of fine sandstones occurring in various levels contain specific echinoderm-dominated faunas assigned to the shallow-water

Fig. 6. (Continued) *Lingulella* Biofacies (*Lingulella* with the first polymeroid trilobites, e.g. *Paradoxides* s.l., *Ellipsocephalus*, *Conocoryphe* and the first very rare agnostid *Peronopsis*). *Lingulella* Biofacies shifted to the Brdy segment of the basin, recovering in the Litavka river valley area until the end of sedimentation of the Jince Formation (i.e. after filling of the Přebram–Jince Basin). (b) Progressive transgression and deepening of the basin characterized by the first appearance of the later dominant polymeroid trilobite Biofacies (*Ellipsocephalus*, *Paradoxides* s.l., *Conocoryphe*, *Ptychoparioides*, *Acadolenus*, *Litavkaspis*), associated with the stepwise onset of agnostid trilobites (*Phalagnostus*, rarely also *Phalacroma*, *Condylopyge*, *Pleuroctenium*) and the first shallow-water echinoderms of the *Asturicystis* and *Ceratocystis* associations [see (d)]. The first obvious affinity to Iberian peri-Gondwana is in polymeroid trilobites (*Acadolenus*), and cinctan and stylophoran echinoderms (*Asturicystis* and *Ceratocystis*). (c) Deepening and differentiation of the basin with the *Lingulella* Biofacies dominating in the shallow-water Brdy area, followed laterally by diverse polymeroid trilobite Biofacies (with *Jincella*, *Ptychoparia*, *Lobocephalina*) and the offshore miomeroid trilobite Biofacies (*Onymagnostus*, *Hypagnostus*, *Doryagnostus* and *Tomagnostus*). Continuous affinity to southwestern Europe of the polymeroid trilobite is interrupted suddenly by the incoming of miomeroid trilobites unknown in Spain, France or Germany, but typical of Baltic and Avalonian regions (Sweden, Norway, Britain, Newfoundland). (d) Substrate-related echinoderm associations occur through a major part of the Jince Formation. The stylophoran *Ceratocystis* is known from Spain and France, as well as from Sweden, whereas the edrioasteroid *Stromatocystites* is restricted to Baltica and Newfoundland. Cinctan echinoderms are known exclusively from Gondwanan Africa, Spain, France, Germany and rarely also in Germany and Britain. The other eocrinoids and the ctenocystid *Etoctenocystis* represent endemic taxa.

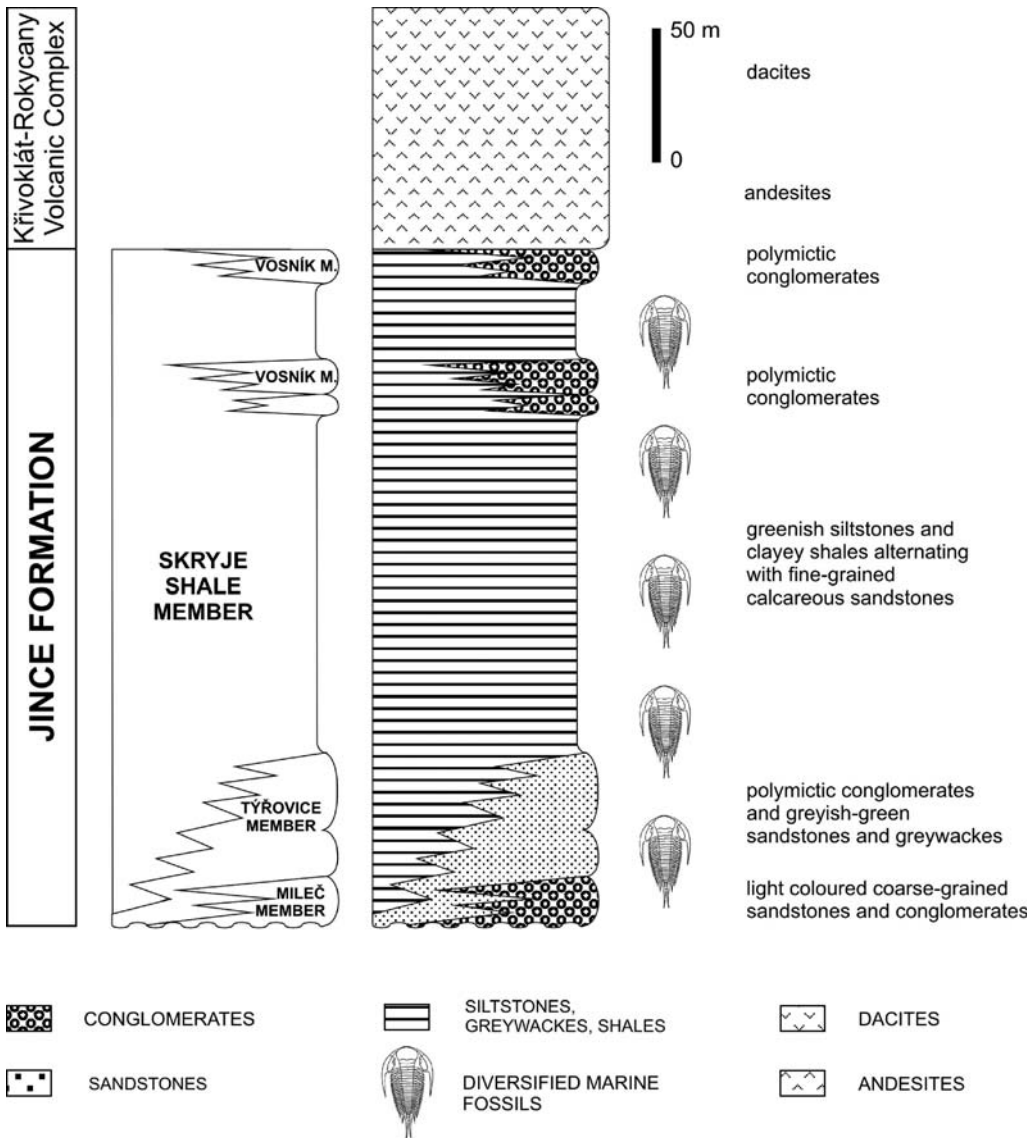


Fig. 7. Stratigraphy of the Cambrian in the Skryje–Týřovice Basin (adopted after Havlíček 1971a; Elicki *et al.* 2008).

Ceratocystis Association (commonly with the polymeroid trilobite *Ctenocephalus*) and/or a slightly deeper-water *Stromatocystites* Association (associated with *Ptychoparia* and *Germaropyge*) (Fig. 9). Similarly, very restricted lenses of greywackes to shales can be characterized by the common occurrence of eocrinoids in the *Lichenoides* Association or ctenocystoid echinoderms in the *Etoctenocystis* Association, both associated with common polymeroid trilobites (e.g. *Skretiaspis*, *Paradoxides s.l.*). The fine shales in higher stratigraphical levels

of the formation are usually dominated by tests of cinctan echinoderms of the *Trochocystites* Association, usually accompanied by large paradoxid trilobites, *Conocoryphe*, *Agraulos*, *Jincella*, *Sao*, *Solenopleurina*, occasionally also with the rare eocrinoid *Luhocrinus* (Fig. 8b).

In the northeastern area of the basin, tongue-like bodies up to several metres thick of the polymict Vosník Conglomerate are developed in the upper part of the sequence. Kukul (1971) interpreted the Týřovice, Skryje and Vosník members as deposits

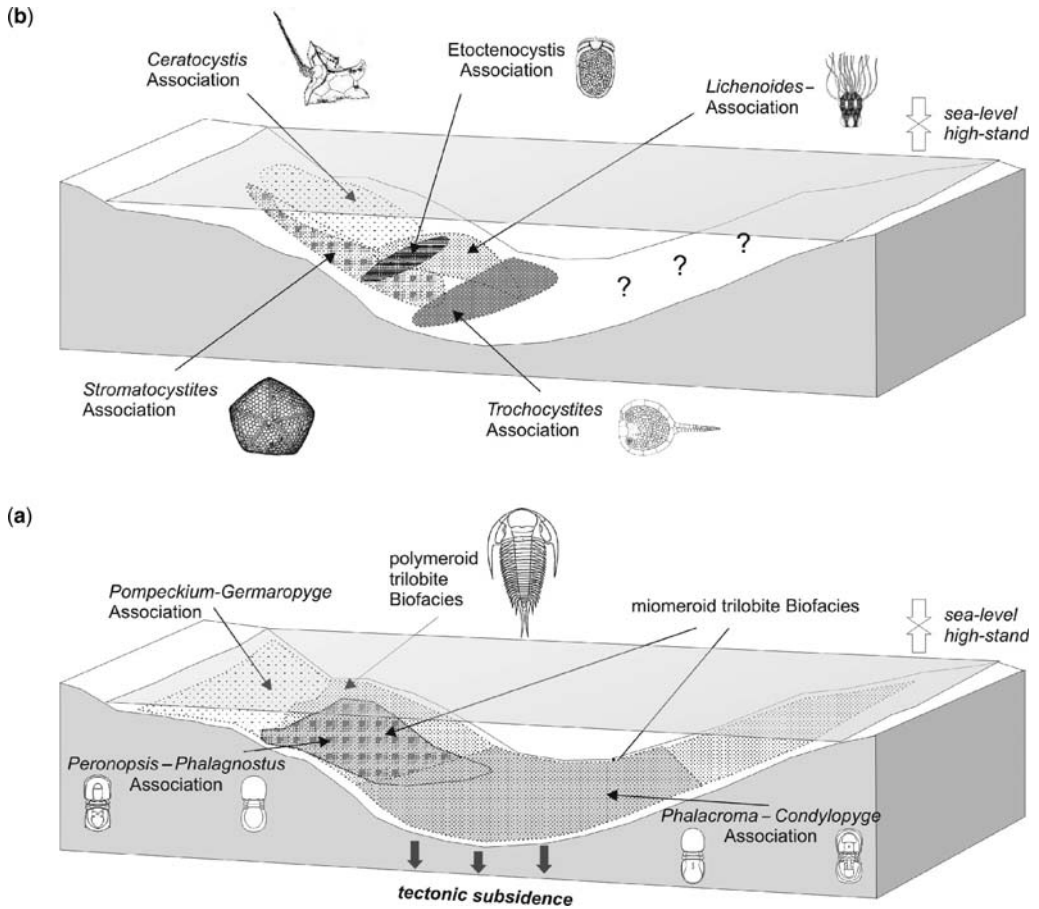


Fig. 8. Diagrammatic history of the Skryje–Týřovice Basin and its faunal associations of the Jince Formation. Only the left (WNW) slope of the basin is mostly illustrated, for simplification. Palaeoecological terminology is adopted from Fatka *et al.* (2006, 2007). **(a)** Beginning of marine ingress near the base of Jince Formation with onset of the endemic *Pompeckium–Germaropyge* Association, followed by progressive deepening of the basin with a stepwise appearance of the polymeroid trilobite Biofacies, associated with the *Peronopsis–Phalagnostus* Association in relatively inshore facies and the *Phalacroma–Condylpyge* Association in the deeper offshore. All the facies were well oxygenated. Numerous trilobite taxa (e.g. *Sao hirsuta*, *Peronopsis umbonata*, *Condylpyge rex*, *Pleuroctenium graulatum*) are common for the Skryje–Týřovice Basin and the Lippertsgrüner Formation of the Franconian Forest as described by Sdzuy (2000). **(b)** As in the Příbram–Jince Basin, echinoderm associations occur through the major part of the Jince Formation and show apparent relation to substrate. The *Ceratocystis*, *Stromatocystites* and *Etoctenocystis* associations are the same as in the Příbram–Jince Basin, being complemented by the *Lichenoides* Association (without any other eocrinoids) and the deeper-water *Trochocystites* Association (locally with the eocrinoid *Luhocrinus*).

related to turbidity currents on steep slopes of the sedimentary basin. Cambrian sediments of the Jince Formation are overlain by extrusive rocks (dacites, andesites and rhyolites) of the Furongian Křivoklát–Rokycany Complex.

The worldwide distributed bivalved crustacean genus *Tuzoia* has an obvious relationship to tropical to warm temperate waters (Vannier *et al.* 2007), as does the enigmatic genus *Wiwaxia* (Fatka *et al.* 2009).

The Cambrian fauna in the Skryje–Týřovice Basin is fairly distinct from that of the Příbram–Jince Basin. It includes several endemic genera of polymerid trilobites (*Ptychoparia*, *Ptychoparioides*, *Solenopleurina*, *Perneraspis*), two miomeroid trilobites (*Diplorrhina* and *Skryjagnostus*; the latter is present also in Siberia; Elicki & Pilolla 2004), and two orthide brachiopods (*Pompeckium*, *Jamesella*). Cambrian hyolithids are too poorly studied to be evaluated in this analysis. The polymerid genera

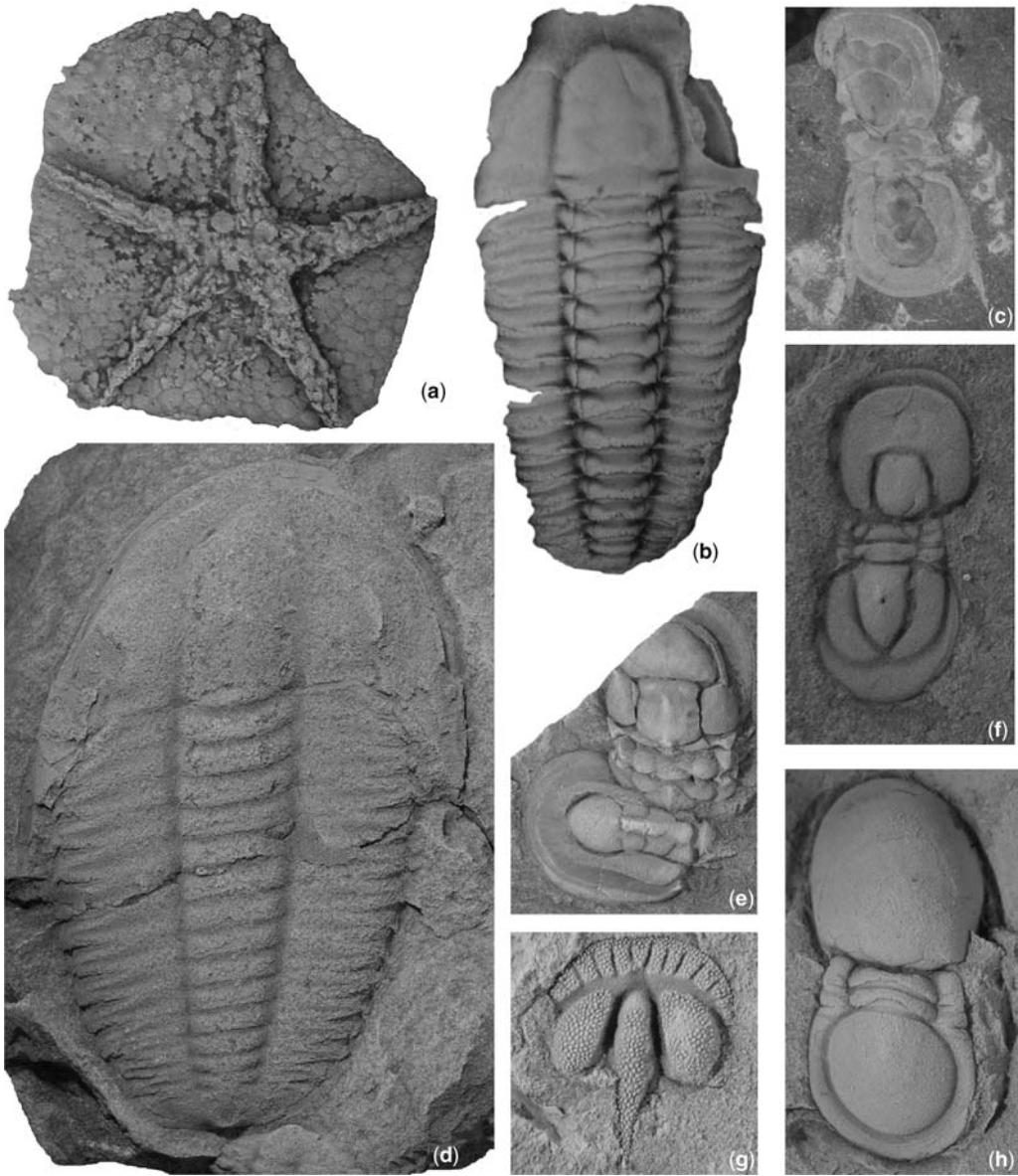


Fig. 9. Characteristic fossils of the 'middle' Cambrian Jince Formation. (a) *Stomatocystites pentangularis*; (b) *Skreiaspis spinosus*; (c) *Pleuroctenium granulatum*; (d) *Germaropyge germari*; (e) *Condylolge rex*; (f) *Hypagnostus parvifrons*; (g) *Dawsonia bohemica*; (h) *Phalagostus nudus*. (a, f, g) Příbram–Jince Basin; (b–e, h) Skryje–Týřovice Basin, all Jince Formation.

Ctenocephalus, *Conocoryphe*, *Agraulos* and *Skreiaspis* occur in different regions of Iberia, Armorica s.s., Turkey and Avalonia. The genus *Sao* has a typically peri-Gondwanan distribution, being known from the Franconian Forest of Germany and the Ossa–Morena Zone of Spain (Gozalo *et al.* 1994). Similarly, *Jincella* is known from Spain, France and Italy (Sardinia).

Železné hory area

Havlíček (1949b), Havlíček & Šnajdr (1951) and Šnajdr (1958) recorded tectonically deformed trilobite fauna from the Senice Shales of the Železné hory area [*Ellipsocephalus*, ?*Paradoxides* (*Eccaparadoxides*), ?*Paradoxides* (*Hydrocephalus*), *Conocoryphe*, *Skreiaspis*, *Lobocephalina*], all known

also from the Jince Formation of both the Příbram–Jince and Skryje–Týřovice basins.

In many respects, very similar Cambrian sequences occur in Germany in the tectonically restricted outcrops of the Franconian Forest (Frankenwald in Bavaria) and the subsurface Delitzsch–Torgau–Doberlug Syncline (see below).

Franconian Forest

In this area most of the Palaeozoic succession shows two distinctly different facies developments, designated as the Bavarian and the Thuringian facies. The autochthonous Thuringian Facies has been supposed to represent a large homogeneous basin, whereas the allochthonous Bavarian Facies is interpreted as the remnants of a much more differentiated basin. However, this distinction has not been recognized in the Cambrian (Elicki *et al.* 2008). The six Cambrian formations overlie different Neoproterozoic units disconformably. Trilobites, brachiopods and echinoderms are reported from the lower part of the 'lower to lowermost middle' Cambrian Tiefenbach Formation. An early 'middle' Cambrian (= early Celtiberian) age is proved by trilobites (*Ornamentaspis*, *Kingaspidoidea*, *Latikingaspis*, *Parasolenopleura*, *Bailiella*, *Paradoxides*, *Acanthomicmacca* and *Wurmaspis*) associated with echinoderms, brachiopods, hyoliths and trace fossils occurring in the following Galgenberg Formation, about 100 m thick. A similar age is supposed also for the Wildenstein Formation, containing a rich trilobite fauna (e.g. *Paradoxides s. l.*, *Condylopyge*, *Bailiella*, *Parasolenopleura*, *Acanthomicmacca*, *Ornamentaspis*, *Kingaspidoidea* and *Dawsonia*) as well as brachiopods, molluscs, echinoderms, sponge spicules and trace fossils. Rare trilobites (e.g. *Conocoryphe* and *Eodiscina*) associated with brachiopods and sponge spicules characterize the sandy to arkosic sediments of the Triebenreuth Formation. Generally rare trilobites (e.g. *Solenopleuroopsis*, *Sao*, *Paradoxides*, *Conocoryphe*, *Condylopyge*, *Parabailiella*, *Bailiella*, *Hypagnostus*, *Peronopsis*, *Phalagnostus*, *Ctenocephalus* and *Acontheus*), cinctan and probably also eocrinoid echinoderms are typical for the mid 'middle' Cambrian (late Caesaraugustian) Lippertsgrün Formation. The late 'middle' Cambrian (Languedocian) Bergleshof Formation is estimated to be less than 100 m thick and contains polymeroid trilobites (*Proampyx*, *Parasolenopleura*, *Holocephalina*, *Bailiella?*, *Jincella*, *Peronopsis*) and one miomeroid trilobite (*Leiagnostus?*) as well as brachiopods, hyoliths and echinoderms.

The fauna of the Lippertsgrün Formation shares several trilobite species known from the Skryje–Týřovice Basin and/or from the Ossa–Morena area of Spain (e.g. *Sao hirsuta*, *Peronopsis*

umbonata, *Condylopyge rex*, *Pleuroctenium granulatum*).

Saxothuringia–Lusatia and NW Saxony

The 'lower' Cambrian succession in this area differs from the development in Bohemia by an apparent dominance of carbonate sedimentation. However, clear similarities do exist in the Delitzsch–Torgau–Doberlug Syncline, where the 'lower' Cambrian Zwethau Formation (composed of shallow-marine carbonates and siliciclastic deposits) is overlain by the 400 m thick fossiliferous Tröbitz Formation, composed of quartzitic sandstones alternating with micaceous claystones containing trilobites (*Paradoxides*, *Condylopyge*, *Ornamentaspis*). The environment has been interpreted as a quiet siliclastic shelf. The overlying 350 m thick sequence of quartzitic sandstones alternating with micaceous claystones with trilobites (*Paradoxides*, *Ellipsocephalus*, *Bailiella*, *Solenopleura*, *Badulesia*, *Condylopyge*) is assigned to the Delitzsch Formation (Buschmann *et al.* 2006). Trilobite taxa are not decisive from palaeogeographical point of view, as almost all of them occur also in Baltica, Britain, Newfoundland and/or Spain and France.

The 'middle' Cambrian faunas from shallow-marine sandstones, siltstones and greywackes are dominated by poor brachiopod associations and/or by moderately diversified trilobite associations. The oldest assemblages consist of typical Mediterranean-type genera clearly indicating the West Gondwanan affinity, namely to some regions in Spain. In younger levels trilobite taxa characteristic of Baltica and Avalonia appear successively. A similar scheme is known from the Franconian Forest (Elicki *et al.* 2008), whereas in the Delitzsch Syncline the poor fossil content excludes discussion of palaeogeographical relationships of this area.

Sources of the Perunica Ordovician fauna

The earliest Tremadocian fauna in the Prague Basin comprises diverse immigrants into the basin. Unfortunately, there is no information about biota from the deeper outer shelf facies surrounding Perunica in this time. The olenid Biofacies is missing in the Prague Basin, and the other deep-water facies of Perunica, most probably present under the Cretaceous in northern Bohemia, are unfossiliferous to very poorly fossiliferous (Fig. 10). In its Ordovician history, the faunas of Perunica were never isolated and never constitute distinctive and endemic and/or clearly different faunas from neighbouring terranes.

Along the West Gondwana periphery, represented mostly by cratonic North Africa, Iberia,

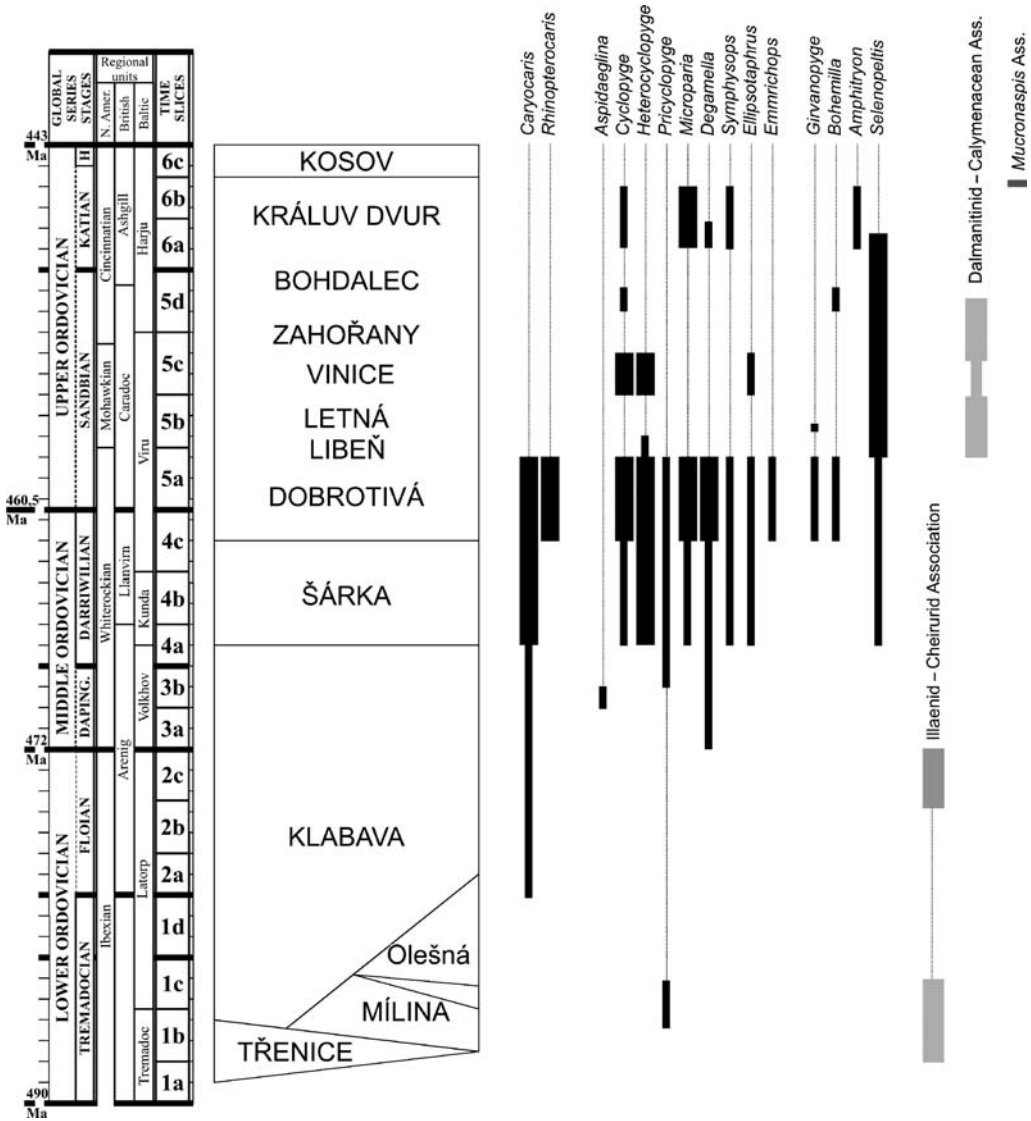


Fig. 10. Stratigraphy of the Ordovician in the Prague Basin (adopted after Havlíček 1982, 1998) with distribution of caryocarids, supposed nektonic trilobites (cyclopygids, remopleurids, *Bohemilla* and *Selenopeltis*) and range of selected trilobite associations (after Chlupáč 1970 and Marek 1961).

Armorica *s.s.*, Thuringia, Perunica and other suspect terranes, there are only scarce data on late Cambrian and early Ordovician shelly faunas (Bassett *et al.* 2002). The brachiopods *Billingisella*, *Protambonites*, *Poramborthis* and possibly also *Jivinella* and a few trilobites are known in Iberia (Havlíček & Josopait 1972; Hammann 1974; Villas *et al.* 1995). *Billingisella* and *Saccogonum* are reported from late Cambrian sandstones of Morocco (Mergl 1983; Mergl *et al.* 1998) but both taxa have nothing in common

with brachiopods of Perunica in the early Ordovician. Early Tremadocian faunas of the Montagne Noire and the Iberian Chains (Courtessole & Pillet 1978; Hammann *et al.* 1982) have olenids, *Angelina*, *Parabolina*, *Triarthrus* and *Shumardia*, which all are missing in Perunica. A small trilobite fauna with *Bavarilla*, *Parapilekia* and *Parabathycheilus* remarkably similar to the fauna of Perunica is reported from Mauritania (Destombes *et al.* 1969). There is increasing evidence that some brachiopods

of Perunica had ancestors and relatives in much more distant regions of Gondwana. New records by Benedetto (2007) from the Precordillera of Argentina indicate, together with the older published data (Havlíček & Branisa 1980) that some brachiopods formerly considered to be typical of Perunica (*Apheoorthina*, *Euorthisima*, *Kvania*, *Poramborthis*, *Robertorthis*) have ancestors in this distant region. Rich 'Dalmanella-shaped small brachiopods' from the Precordillera are representatives of the initial orthide radiation, which took place in a temperate climate and in neighbouring Laurentia. A similar seaway may be proposed for ancestors of other early Ordovician orthid brachiopods of Perunica, namely *Apheoorthina*, *Eoorthis* and the billingsellacean *Protambonites*. Havlíček (1949a, 1977) noted that the closest relatives of these genera should be sought among the Late Cambrian brachiopods of Laurentia. Some of these genera (*Jivinella*, *Euorthisima*) reached low-latitude South China as early as in the Arenig.

Large lingulate brachiopods, which are a dominant component of the earliest shallow-water benthic association in Perunica, were probably derived from a low-diversity lingulate fauna in cratonic basins of West Gondwana. Shallow-water lingulate brachiopod faunas of the late Cambrian and early Ordovician in Baltica, containing *Ungula*, *Obolus*, *Schmidites*, *Helmersenina*, etc. (Popov *et al.* 1989) are very different from the fauna of Avalonia, the ATA, and Perunica, indicating the existence of an ocean barrier wide enough to prevent larval passage and successful settling in this time. The late Cambrian and early Ordovician successions of cratonic West Africa and the ATA contain low-diversity associations with large lingulates, partly reviewed by Cocks & Lockley (1981) and Havlíček (1989). Some of them are probable ancestors of the remarkably rich lingulate brachiopod fauna of Perunica.

A remarkably rich suite of micromorphic lingulate brachiopods appeared in late Tremadocian and early Floian times (Fig. 11b). This fauna, living on fine sands in a subtidal environment, shows remarkably high diversity and is very similar to the *Leptembolon* Fauna reported originally from the St. Petersburg area (Gorjansky 1969) and the Holy Cross Mountains of Poland (Bednarczyk 1964). Also, some micromorphic brachiopods of the Björkasholmen Limestone (*Pomeraniotreta*, *Myotreta*, *Dactylotreta*, *Elliptoglossa*, *Siphonotretella*, etc.) of south Scandinavia (Popov & Holmer 1994) are common in the *Leptembolon* Fauna of Perunica (Mergl 2002). A fauna with common *Hyperobolus* is also known from slightly younger strata in the South Urals (Popov & Holmer 1994). The geographical distribution of these lingulate brachiopod-dominated faunas indicates easy dispersion of

brachiopods, similar climatic conditions and reduction of geographical barriers between Perunica and facing margins of Baltica in the late Tremadocian–Floian interval.

Unlike lingulate brachiopods, the earliest rhynchonelliformean brachiopod faunas of Perunica contain eorthids of restricted occurrence (*Robertorthis*, *Apheoorthina*, *Jivinella*), but also early plec-torthis that are abundant in the late Cambrian and Tremadocian of Argentina (*Kvania*). Syntrophiids (*Poramborthis*) and billingsellids (*Protambonites*) have relatives in the Iberian Peninsula and South Urals (Popov *et al.* 2001). Other orthid taxa present in Perunica (*Ranorthis*, *Angusticardinia*) are known in younger beds in the Lower Ordovician successions of Estonia and the St. Petersburg area. The similarity is thus merely a mixing of Gondwanan taxa, some of which reached Baltica near the end of the Early Ordovician. The brachiopod fauna indicates a somewhat mild climate in Perunica in the Tremadocian and Floian.

The first Ordovician trilobites appeared in Perunica together with the earliest eorthids, plec-torthis and diverse lingulates in the Late Tremadocian. The illaenimorph *Hemibarrandia*, the large cheirurid *Parapilekia*, and the probable eurekaid *Holubaspis* were dominant in the remarkably diverse trilobite assemblage. Apart from the cosmopolitan *Apatokephalus*, *Ceratopyge*, *Dikelo-kephalina*, *Harpides*, *Proteuloma*, *Platypeltoides* and *Geragnostus*, there are genera of likely Gondwanan origin. *Agerina* is known from Argentina, Bavaria and Sweden. *Anacheirurus* has been reported from Bavaria, Spain and England. The endemic Gondwanan *Bavarilla* has been reported from Bavaria and Mauritania, and *Parabathycheilus* is known from Spain, Bavaria and Mauritania, but extended to China in the Arenig. There are only a few truly endemic taxa in Perunica. The orometopid *Celdometopus* is most similar to the rare Baltic *Pagometopus*. The earliest known lichids *Holoubkovia* and *Lichekephalus* are endemic. *Holoubkocheilus* and *Pharostomina* show close affinity to other ancient Gondwanan calymenaceans. In its overall composition the trilobite fauna of the Tremadocian is closely comparable with the illaenid–cheirurid Biofacies of the low-latitude early Ordovician (Fortey 1975), but the *Hemibarrandia*–*Parapilekia* Association of Perunica is complemented by calymenacean taxa and the earliest cyclopygids. These two latter groups clearly identify the Gondwanan affinity of Perunica trilobite associations, but also the opening of its shelves to incidental immigrants from neighbouring areas (Sdzuy *et al.* 2001).

The Floian and Dapingian brachiopod faunas of Perunica retain some endemic elements (*Jivinella*, *Poramborthis*, *Prantlina*, *Nocturnellia*, *Ferrax*,

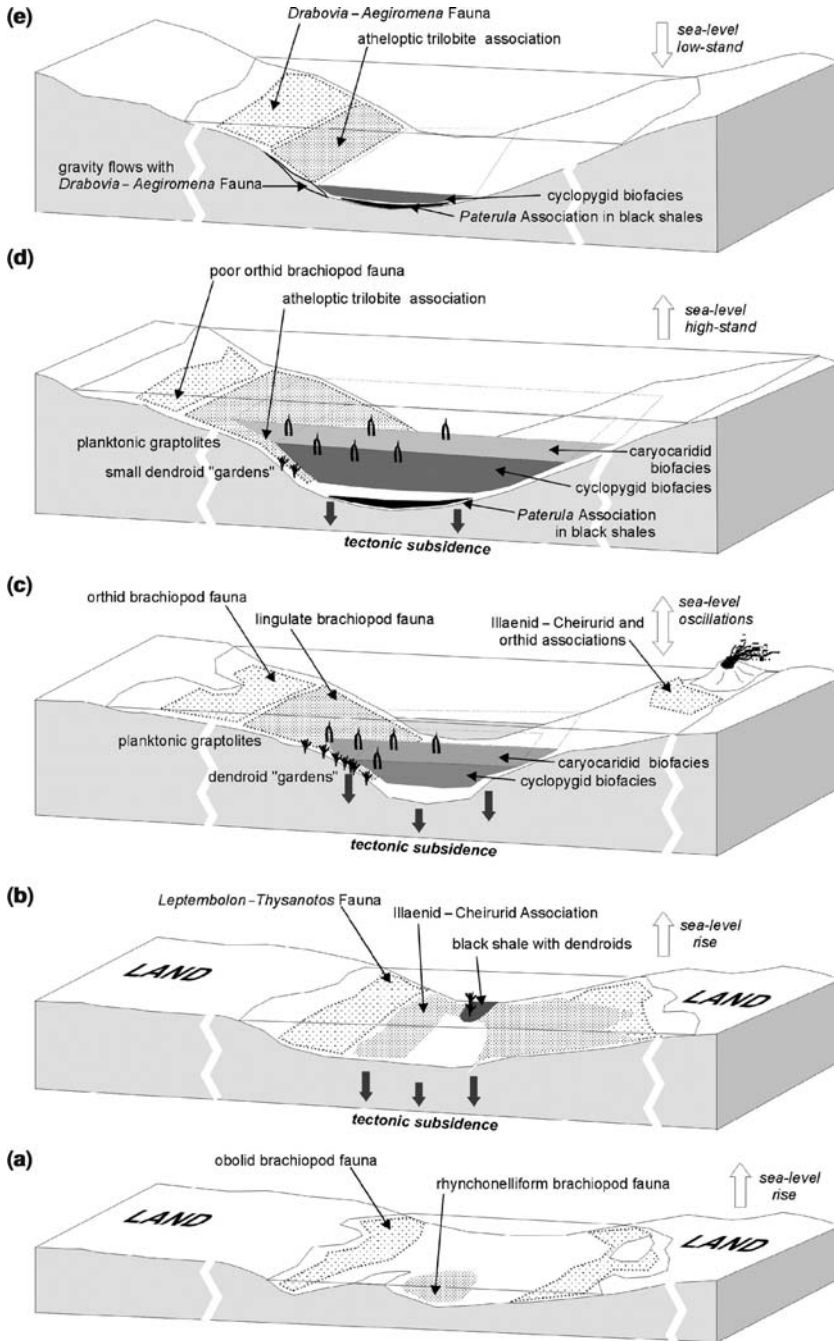


Fig. 11. Diagrammatic history of the Prague Basin and its faunal associations of the Ordovician to early Silurian. Only the left (NW) slope of the basin is mostly illustrated, for simplification, for simplification. Palaeoecological terminology is adopted from Chlupáč (1965), Havlíček (1982), Štorch & Mergl (1989), Mergl (1999), Štorch (2001) and Mergl *et al.* (2007). (a) Early(?) and Middle Tremadocian: Třenice Formation. Transgression with the onset of lingulate brachiopod associations (*Hyperbolus* Community, *Westonisca* Community) and poor rhynchonelliform brachiopod associations (*Poramborthis* Community). Affinity to other Gondwanan faunas. (b) Late Tremadocian and Floian: Mílina Formation and Olešná Member of the Klabava Formation. Transgression and deepening of the basin associated with

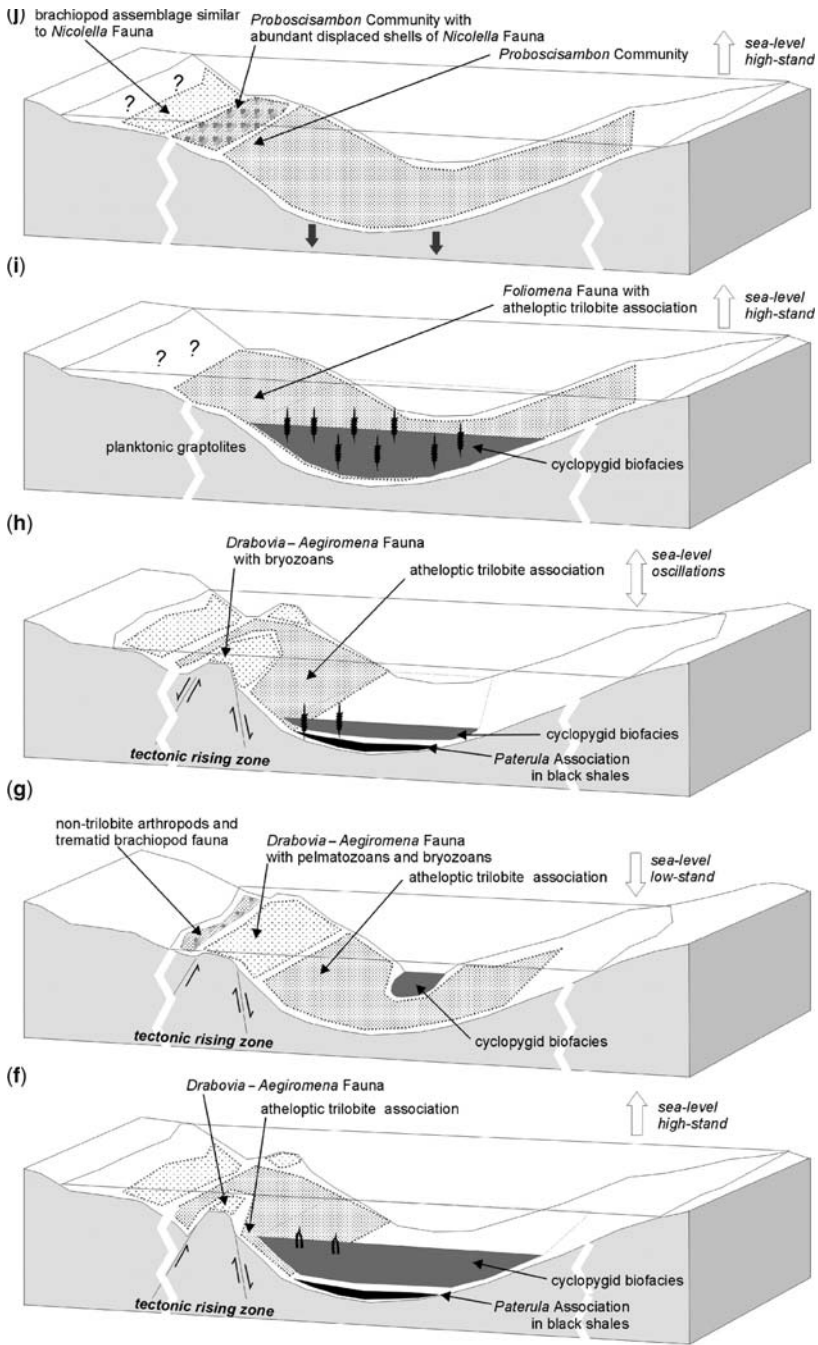


Fig. 11. (Continued) diverse lingulate brachiopod associations (*Leptembolon–Thysanotos* Association), diverse trilobite associations (*Hemibarrandia–Parapilekia* Association and a deeper *Proteuloma–Ceratopyge* Association) and black shales with dendroids in NE part of the basin. Affinity both to Baltic and West Gondwanan fauna. (c) Dapingian: Middle and Upper Klabava Formation. Deepening and differentiation of the basin with diverse lingulate and rhynchonelliform brachiopod associations (*Acrotreta* Community, *Rafanoglossa* Community, *Nocturnellia* Community, *Nereidella* Community), diverse trilobite associations (*Pliomerops* Association, Asaphid Association, and the offshore *Euloma* Association); rich benthic dendroid 'gardens', diverse planktonic graptolites, and Caryocaridid and

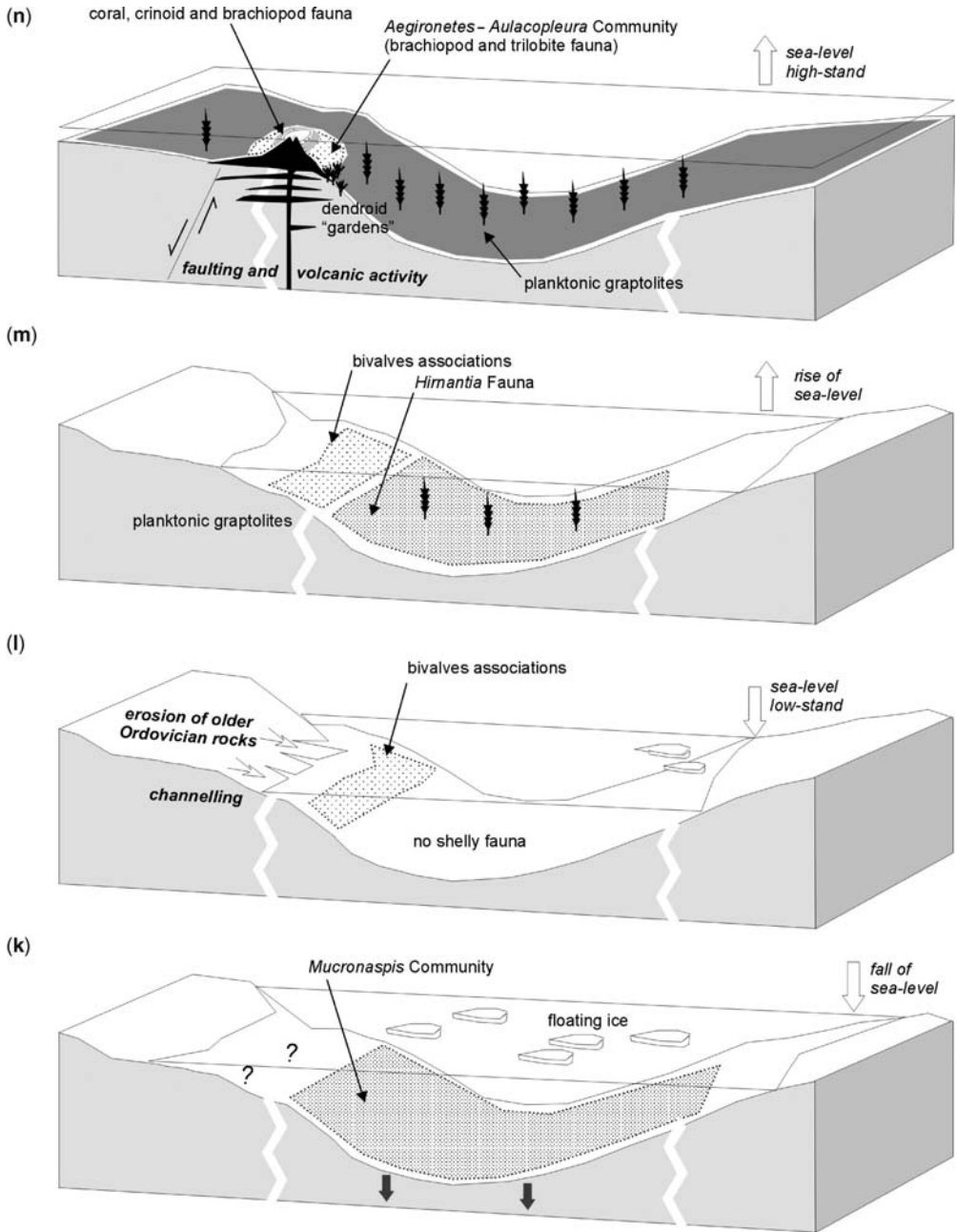


Fig. 11. (Continued) Cyclopygid Biofacies. High endemicity and decreasing influence of Baltic fauna. (d) Darrivilian: Šárka and Dobrotivá formations. Maximum deepening and differentiation within the basin, with the onset of poorly oxygenated waters. Early *Aegiromena*–*Drabovia* Fauna with poor 'brachiopod' association (*Tigillites* Community with *Tissintia* and *Tafilaltia*), offshore brachiopod *Euorthisina* Community and *Paterula* Community, atheloptic trilobite association (*Placoparia* Community); poor benthic dendroid 'gardens', poor planktonic graptolites, and peak of both the Caryocaridid and Cyclopygid biofacies. Increasing influence of Gondwanan fauna. (e) Early Sandbian: Libeň Formation. Shallowing of the basin, the onset of mature quartzitic inshore sands and poorly oxygenated waters in deep offshore. *Aegiromena*–*Drabovia* Fauna with rich brachiopod association (*Drabovia* Community) and the inshore trilobite Dalmanitid–Calymenacean Association, the poor offshore atheloptic trilobite association, and the

Styxorthis), but with an abundance of *Nereidella* and *Ranorthis* in shallow lithofaces, genera described originally from South China and Baltica, respectively, demonstrating a more cosmopolitan character of the fauna. As mentioned above, *Poramborthis* is characteristic of the Tremadocian brachiopod fauna of Perunica but it also persisted to the Dapingian. This genus was described as an aberrant orthid (Havlíček 1949a, 1977) but now (unpublished) it is considered to be an early syntrophiid close to *Tetralobula*, which is characteristic of Baltica and Laurentia. The presence of *Protambonites*, early syntrophiids and common taxa of the *Thysanotos* Fauna (including *Leptembolon* and *Thysanotos*, diverse micromorphic brachiopods such as *Dactylo-treta*, *Pomeraniotreta*, *Acrotreta*, *Numericoma*, *Elliptoglossa*, the siphonotretids *Eosiphonotreta*, *Siphonotretella*, *Alichovia*, etc.) demonstrate a relationship to the Early and early Middle Ordovician fauna of Baltica, reviewed thoroughly by Popov & Holmer (1994), Egerquist (2004) and others. Stratigraphical records of the *Leptembolon*–*Thysanotos* Fauna in Perunica predate the South

Urals and East Baltic occurrences. Perunica seems to have occupied an intermediate position between Gondwana and Baltica in the Early Ordovician. *Thysanotos* and allied faunas probably originated in this peri-Gondwanan area, but *Thysanotos* as well as *Leptembolon* are unknown from the cratonic shelves of Gondwana (exemplified by North Africa) or Armorica. Perunica shelves were sources for later and generally brief passage of this fauna in nearby facing margins (the South Urals), and even more distant parts of Baltica (present East Baltic and the Holy Cross Mountains) and other distant terranes (Iran).

A unique trilobite fauna from the middle part of the Klabava Formation, dated approximately near the Floian and Dapingian boundary, and containing *Pliomerops*, *Ectillaenus*, *Cyrtometopus* and other aberrant but poorly known taxa (*Pseudopetigurus*, *?Holubaspis*) are also suggestive of temperate illaenid–cheirurid associations (Fig. 11c). However, the faunal similarity between Perunica and Baltica decreased from the beginning of the Middle Ordovician. A rich Volkhov age brachiopod

Fig. 11. (Continued) Paterula Community; absence of graptolites and poor Cyclopygid Biofacies. High affinity to Gondwanan fauna. (f) Early Middle Sandbian: Vinice Formation. Highstand of sea level and tectonic differentiation of the basin, shoals on tectonically rising zones, and poorly oxygenated waters in deeper offshore. A rich *Aegiromena*–*Drabovia* Fauna (*Bicuspina* Community), less diverse trilobite Dalmanitid–Calymenacean Association on shoals and atheloptic trilobite association with *Paterula* Community in deeper offshore; poor planktonic graptolites and Cyclopygid Biofacies. High affinity to Gondwanan fauna. (g) Early and late Middle Sandbian: Letná and Zahořany formations. Shallowing of the basin, quartzitic sands and greywackes inshore, siltstones offshore. *Aegiromena*–*Drabovia* Fauna with rich brachiopod associations (*Drabovia* Community, *Bicuspina* Community), non-trilobite arthropods and trilobite Dalmanitid–Calymenacean Association inshore, and a poor atheloptic trilobite association offshore; rare graptolites and Cyclopygid Biofacies. High affinity to Gondwanan fauna. (h) Late Sandbian: Bohdalec Formation. Sea-level oscillations and tectonic differentiation of the basin, shoals on tectonically rising zones, and poorly oxygenated waters in deeper offshore. A rich *Aegiromena*–*Drabovia* Fauna on shoals (*Hirnantia* Community of the so-called Polyteichus facies), less diverse benthic communities in moderately deeper environment (*Svobodaina* Community) with poor trilobite Dalmanitid–Calymenacean Association and atheloptic trilobite association with *Paterula* Community in deep offshore; poor planktonic graptolites and poor Cyclopygid Biofacies. High affinity to Gondwanan fauna. (i) Katian: Králův Dvůr Formation. Highstand of sea level and well-oxygenated waters in deep offshore. Inshore fauna unknown. *Foliomena* Fauna (*Rafanoglossa* Community) and atheloptic trilobite association in deep offshore; abundant planktonic graptolites and rich and latest Cyclopygid Biofacies. Manifestation of the Boda event with the onset of temperate (e.g. Baltic) fauna. (j) Late Katian (Rawtheyan): uppermost Králův Dvůr Formation. Initiation of regression, well-oxygenated waters in deep offshore. Inshore fauna unknown, but represented by displaced shelly material. A diversified equivalent of the *Foliomena* Fauna (*Proboscisambon* Community), rich atheloptic trilobite association in deep offshore; absence of graptolites and cyclopygids. Termination of the Boda event combined with a clear affinity to temperate (e.g. Baltic) fauna. (k) Early Hirnantian: topmost Králův Dvůr Formation. Rapid regression, well-oxygenated waters in deep offshore. Inshore fauna unknown. Poor trilobite–ostracode fauna (*Mucronaspis* Community) with rare small brachiopods; absence of graptolites and cyclopygids. Initiation of glaciation followed by diamictite deposition, expressed by a cosmopolitan West Gondwana derived fauna. (l) Middle Hirnantian: Upper Kosov Formation. Maximum regression, erosion of older Ordovician rocks in coastal area. Inshore fauna unknown except bivalves in sandstones. Maximum glaciation, no palaeogeographical data. (m) Late Hirnantian: top of the Kosov Formation. Rapid sea-level rise, well-oxygenated waters in deep offshore. Inshore fauna of bivalves in sandstones. Taxonomically rich *Hirnantia* Fauna (*Hirnantia saggitifera* Community) with trilobites, bryozoans, gastropods etc.; planktonic graptolites rarely present. West Gondwana derived fauna showing affinity to low-latitude palaeocontinents. (n) Middle Llandovery: Želkovice Formation. Sea-level fall within general sea-level highstand, with benthic fauna on volcanogenic elevations above surrounding and poorly oxygenated waters of deeper sea. Taxonomically rich trilobite–brachiopod fauna (*Aegironetes*–*Aulacopleura* Community) with some elements of the *Hirnantia* Fauna, shallow-water crinoids and corals; rich dendroid 'gardens' and abundant and diverse planktonic graptolites in deeper, open-water sites. Probably West Gondwana derived fauna with many new subtropical elements.

fauna of the Baltic area is very diverse and different (Egerquist 2004).

Other evidence relating to the Early Ordovician affinity of Baltica and Perunica can be shown also with other invertebrate groups. Cystoids (*Echinosphaerites*, *Glyptosphaerites*, *Aristocystites*, *Palaeosphaerites*), the gastropods *Mimospira* and *Modestospira*, the ascidian tunicate *Palaeobotryllus*, trepostomate bryozoans and ostracodes present in Perunica suggest a mild to temperate climate in the Early and early Middle Ordovician. One case of such a rich fossil association, the earliest brachiopod–bryozoan–pelmatozoan association reported from Ejpovice near the top of Dapingian (Mergl 2004), is a remarkable mixture of archaic lingulate brachiopods (e.g. *Orbithele*) with younger elements (bryozoans, hyolith *Quadrotheca*, gastropod *Mimospira*, etc.). At this time these taxa had their relatives in Baltica or other continents of the subtropical zone. In West Gondwana these genera are rare or absent. Palaeolatitudinal data for the late Cambrian and early Ordovician position of Perunica, despite some controversy (Tait *et al.* 1994; Krs & Pruner 1999), indicate low latitude at about 30°S (Krs *et al.* 1986a, b). Lithological criteria support a temperate climate in Perunica in the Early and early Middle Ordovician (see discussion by Havlíček 1999). Sedimentological data indicate intensive chemical weathering on the nearby land. There are abundant hematite beds in shallow-water sediments, with stromatolitic layers and rapid deposition of immature sands with hematite cement from nearby land. It is notable that rather diverse but as yet unstudied associations of conodonts occur in the Floian deposits of the Prague Basin (Fig. 11b). Younger, early Middle Ordovician rich conodont associations with some Baltica-related taxa (*Barrandegnathus*; Stouge 2005) have been described by Dzik (1983) from beds of late Arenig age (upper Klabava Formation below the late Arenig *Desmochitina bulla* Chitinozoan zone; Paris & Mergl 1984). Early to Late Ordovician chitinozoan assemblages contain typical peri-Gondwanan taxa (Paris 1990; Dufka & Fatka 1993; Fatka 1993). Abundant conodonts in the various lithofacies of the Klabava Formation could indicate mild or temperate climate.

The Mediterranean character of acritarch assemblages has been recognized by Vavrdová (1974a, 1997). The diverse late Early to Middle Ordovician acritarch assemblages contain typical peri-Gondwanan taxa (e.g. *Aureotesta* Vavrdová 1972; see Brocke *et al.* 1998; *Arbusculidium* Deunff 1968; see Fatka & Brocke 1999; *Dicrodiacrodium* Burmann 1968; see Servais *et al.* 1996; *Frankea* Burmann 1968; see Fatka *et al.* 1997) known from numerous localities in Gondwanan Africa and peri-Gondwanan Europe, and generally absent in

Baltica (Brocke *et al.* 1995; Servais & Fatka 1997; Servais *et al.* 2000).

Middle Ordovician faunal turnover

Turnover of the faunal composition took place in Perunica during the Darriwilian (Šárka and Dobrotivá formations). Above the Šárka Formation, in the Dobrotivá Formation and especially with the beginning of sedimentation of the Libeň Formation, the trilobite and brachiopod faunas show considerable similarity to Armorican and other West Gondwanan faunas. However, the typical shallow shelf Gondwanan *Neseuretus* Biofacies never expanded as far as Perunica.

In Perunica, the first extensive onset of shallow subtidal ferrous sedimentation in the early Darriwilian was followed by sedimentation of mature quartzitic sands in shallow inshore shelf areas. Both lithofacies passed basinwards into thick clay sequences on a deep basinal floor, an environmental equivalent to an outer shelf (Fig. 11d). This situation persisted more or less continuously from the late Darriwilian to the very end of the Katian. During a highstand of sea level, continuous sedimentation of black shales in the basin was interrupted in its later stages by slumps of sands from shoals. The sands brought shelly material from shallower environments into different and often poorly oxygenated deep environments of the basinal floor. In lowstand periods the sandy beaches moved basinwards, and submarine elevations in tectonic-rising zones were eroded and/or formed small shoals suitable for occupation by relatively shallow-water brachiopod–bryozoan–pelmatozoan associations (Havlíček 1982). Sea-level changes were probably controlled by glacioeustasy combined with tectonism during the late Middle and early Late Ordovician, but unambiguous glaciomarine deposits are unknown in Perunica until the Hirnantian (Brenchley & Štorch 1989). Proliferation of the Early Ordovician epibenthic shallow-water lingulate brachiopod associations stopped from the beginning of the Darriwilian. Bivalves became significant at the same time on the shelves of both Gondwana and Perunica (Babin 1993). Such a reorganization of benthic associations is known also in other areas (Sanchez & Waisfeld 1995; Bassett *et al.* 1999; Sanchez *et al.* 1999; Popov *et al.* 2007) but in Perunica it also resulted in dramatic lithological change. The onset of pure quartzitic sands less suitable for infaunal lingulates began at this time. Only the large trematids *Drabodiscina*, *Trematis* and *Ptychopeltis* remained common in very shallow-waters, being often fixed to hard substrates. In the early Darriwilian, rhynchonelliform brachiopod associations were taxonomically

poor, based on immigrants from the West Gondwanan territory. *Eodalmannella* and *Euorthisina* are present exclusively in the deep-water environment of the Šárka Formation. *Brandysia* and *Benignites* are restricted to a similar environment of the Dobrotivá Formation, but the former is reported from deep-water deposits of North Spain (Gutiérrez-Marco *et al.* 1996). *Eodalmannella* was probably derived from the earlier local *Ranorthis*. *Euorthisina* shows much extensive stratigraphical and geographical distributions. It has been reported from the Early and early Middle Ordovician of Bolivia, Avalonia, Iberian Peninsula and cratonic North Africa (Havlíček 1971b; Havlíček & Branisa 1980; Robardet & Gutiérrez Marco 2004), but also from South China (Xu & Liu 1984), indicating its restriction to extensive and exclusively peri-Gondwanan regions. *Euorthisina* has never been reported from Baltica or other continents.

In the late Darriwilian and early Sandbian, the benthic faunas of Perunica became dominated by brachiopods of nearby Gondwanan origin. Heterorthis, draboviids, plectorthis and the plectambonitid *Aegiromena* became significant on the shallow shelves. *Tissintia* and/or *Tafilaltia* are reported from the late Darriwilian of more terranes (Armorica, Avalonia, NW Africa, Perunica; Havlíček 1971b, 1977; Villas 1985, 1992, 1995; Mélou *et al.* 1999). The next rapid geographical spread of mostly orthid-dominated, and probably cold-water-related brachiopod fauna, in Havlíček's (1989) definition the *Aegiromena*–*Drabovia* fauna, culminated in the Sandbian Stage. Many genera including the eponymous *Drabovia* and *Aegiromena* became widespread across cratonic West Gondwana and adjacent terranes, extending as far as Argentina and Bolivia (Havlíček & Branisa 1980), indicating a breakdown of geographical barriers. *Chrustenopora*, *Drabovia*, *Drabovinella*, *Gelidorthis*, *Hirnantia*, *Heterorthina*, *Heterorthis*, *Jezerica*, *Onniella*, *Saukrodictya*, *Svobodaina*, *Bicuspina* and *Aegiromena* are among the most significant taxa. These genera are represented in separate terranes and at particular stratigraphical levels by closely related but endemic species to the very end of the Katian. There are, however, genera with closely restricted occurrences and some of them are genuine endemics of cratonic Gondwana or neighbouring terranes in the Middle and early Late Ordovician. The orthid genera *Appollonorthis*, *Atlantida*, *Cacemia*, *Cilinella*, *Crozonorthis*, *Destombesium*, *Irhirea*, *Reuschella*, *Tarfaya* and *Tazarinia* have very restricted distributions, probably controlled by climatic gradients. Most of these never reached Perunica and only *Cilinella* is endemic in the Prague Basin. In the *Aegiromena*–*Drabovia* Fauna, other groups of rhynchonelliform brachiopods are less common. There are some

rhynchonellids (*Rostricellula*), triplesiids (*Bicuspina*), plectambonitids (*Urbimena*) and strophomenids (*Rafinesquina*, *Blyskavomena*). The faunas of Perunica lack these taxa, with the exception of the almost cosmopolitan *Rafinesquina*. On the other hand, *Onniella* is unknown from Armorica and cratonic peri-Gondwana but it is common in Perunica and Avalonia. The similar but unrelated *Onnizetina* is present in Perunica and is reported later, in the late Katian, from the Carnic Alps (Havlíček *et al.* 1987).

Records of deep-water brachiopods are generally rare in preserved regions of Perunica, being represented by rare small lingulates among which *Paterula* is dominant, associated with small endemic plectambonitids (*Benignites*, *Urbimena*, *Sentolunia*). The presence of *Paterula* unambiguously indicates a deep, outer shelf environment; it is a genuine cosmopolitan genus, present along margins or in deep intracratonic basins of Laurentia, Baltica, South China, Avalonia and Perunica from the early Middle Ordovician to Middle Devonian (Mergl 1999).

The Middle Ordovician trilobite fauna of Perunica (Figs 12–14) is an example of the Dalmanitid–Calymenacean Fauna (Cocks & Fortey 1988). There are many genera in common with Armorica and cratonic Gondwana, but unlike the latter, trilobites known from the Prague Basin are generally of much deeper, offshore character. For instance, there are no records of the *Neseuretus* Fauna in Perunica. The *Neseuretus* Fauna is a typical inshore peri-Gondwanan fauna, known from a huge area in the late Middle Ordovician (see Cocks & Fortey 1988). A similar fauna is known even from low latitudes (Turvey 2002, 2005). The trilobites of the Šárka and Dobrotivá formations mostly belong to the atheloptic association of a deeper outer shelf (Havlíček & Vaněk 1990, 1996). This fauna has some common elements with an older fauna of the Montagne Noire and Wales (Dean 1966; Fortey & Owens 1978, 1987). Similarity should indicate easy exchange of mobile benthos along deep shelves and an ability to cross narrow barriers between small separate terranes (Avalonia, Armorica, Perunica and margins of cratonic West Gondwana). Migration of shelf biota between Perunica and Armorica has been noted by various workers, and the significance of currents has been emphasized (e.g. Gutiérrez-Marco & Rábano 1987; Gutiérrez-Marco *et al.* 1999). However, there are also significant differences. Apart from the typical and widespread peri-Gondwanan *Selenopeltis* and the genera *Placoparia*, *Ormathops*, *Colpocoryphe*, *Ectillaenus*, *Uralichas*, *Eoharpes*, etc., there are endemic taxa. Of them, the trinucleid *Trinucleoides reussi* is very abundant in the Šárka Formation. This genus is unknown outside Perunica and indicates that there were geographical barriers controlling

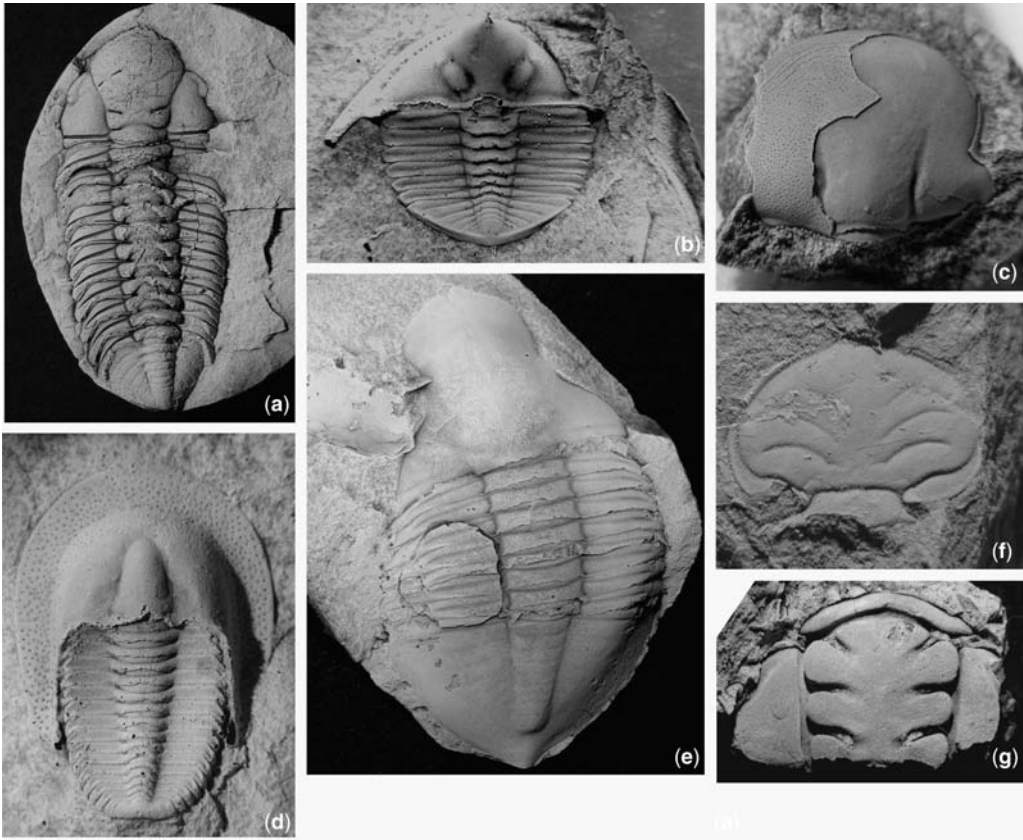


Fig. 12. Characteristic trilobites of the Dapingian (g), Darriwilian (a, b, d, e) and Katian (c, f) of Perunica. (a) *Ormathops atavus*, MBH 569, LS = 37 mm; (b) *Trinucleoides reussi* MBH 677, LS = 11 mm; (c) *Stenopareia oblita* PCZCU 1674, LS = 6 mm; (d) *Eoharpes benignesis* MBH 328, LS = 22 mm; (e) *Megistaspis aliena* MBH 9835, LS = 47 mm; (f) *Amphytrion radians* PCZCU 1673, LS = 6 mm; (g) *Pliomerops lindaueri* PCZCU 1672, LS = 15 mm. (a, b, d) Osek; (c) Levín; (e) Šárka; (f) Praha, Rajtknechtka; (g) Hlava u Komárova. LS, length of specimen.

the spread of benthic, deep-water taxa in the Middle and early Late Ordovician. This restriction demonstrates that deeper shelf conditions were not continuous from Perunica toward the margins of the Gondwana landmass, and barriers were effective in controlling the spread of at least some deep-water taxa. Because climatic barriers are poorly manifested in a deep shelf environment, deep oceanic currents or a greater geographical distance between Perunica and other peri-Gondwanan terranes can possibly be invoked as a barrier. Typically deep-water outer shelf trinucleids are represented by endemic species in Perunica. The restricted occurrence of the orometopid *Celdometopus klouceki* is known already in the Tremadocian. *Bergamia agricola* and *Bergamia praecedens*, and similarly *Trinucleoides reussi* and *T. hostapulp*, are present in the Darriwilian. *Declivolithus alfredi*, *Marrolithus ornathus* and other species occur in the Sandbian,

and *Marekolithus kosoviensis* is restricted in the Katian. High endemicity in species levels also existed among other trilobite groups of Perunica in the Sandbian and Katian (Šnajdr 1955). Shallow-water, sandy subtidal plains had suites of abundant phacopids (*Dalmanitina*, *Ormathops*, *Zeliszella*), calymenaceans (*Calymenella*, *Colpocoryphe*, *Platycoryphe*, *Prionocheilus*), illaenids (*Cekovia*, *Stenopareia*, *Zbirovia*), cheirurids (*Actinopeltis*, *Eccoptochile*, *Eccoptochiloides*) and locally also trinucleids (*Onnia*) and odontopleurids (*Selenopeltis*, *Primaspis*). Unlike in Armorica and cratonic Gondwana, important shallow-water, inner shelf genera such as *Crozonaspis*, *Nesuretus*, *Eohomalonotus*, *Kerformella*, *Salterocoryphe*, *Ogyginus*, etc. are absent in Darriwilian and Sandbian of Perunica. Their absence, and the endemic offshore trinucleids in the Prague Basin, indicate that some trilobite groups were not able to cross the barrier between

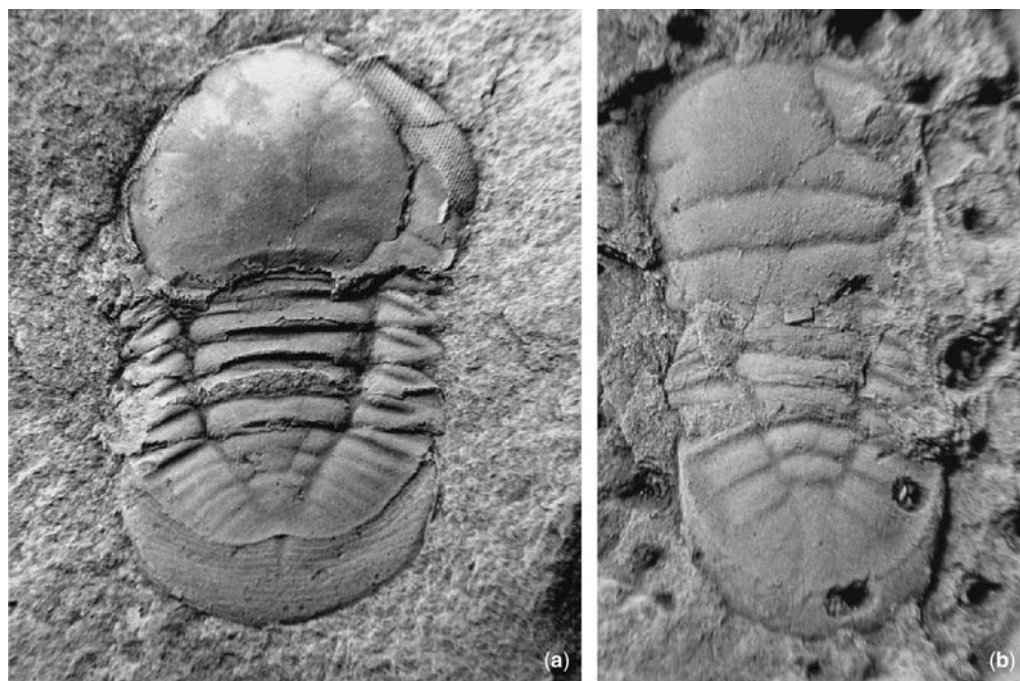


Fig. 13. Cyclopygids of Darriwilian age of Perunica. (a) *Microparia brachycephala* MBH 11659, LS = 14 mm; (b) *Ellipsotaphrus monophthalmus* MBH 328, LS = 8 mm. Both Dobrotivá Formation, Sedlec (Sutice).

Perunica and cratonic Gondwana and adjacent Armorica. In contrast to the Early Ordovician, the benthic macrobenthos of Baltica is very different from that of Perunica in the Middle Ordovician (see Cocks & Fortey 1998; Fortey & Cocks 2003).

The Boda event in Perunica

A change in the benthic fauna of West Gondwana and Perunica took place following the climatic event in the Katian (near the Caradoc–Ashgill boundary). The warming event in the West Gondwanan area (Boucot *et al.* 2003), also named the Boda event (Fortey & Cocks 2005) brought many shallow-water taxa from the temperate zone southwards towards the landmass of Gondwana. The brachiopods *Cliftonia*, *Dolerorthis*, *Eoanastrophia*, *Hedstroemina*, *Iberomena*, *Leangella*, *Leptaena*, *Longvillia*, *Mcewanella*, *Nicolella*, *Oxoplecia*, *Porambonites*, *Ptychopleurella* and *Triplesia* appeared for the first time in terranes located near or on the platform of West Gondwana (Havlíček 1981; Villas 1985; Mélou 1990; Leone *et al.* 1991). This *Nicolella* Fauna is also rich in other macroinvertebrates, with trilobites, ostracodes, machaeridians, bryozoans, cystoids and other groups. Conodonts are reported from Libya, the Iberian Chains, the Armorican Massif and Sardinia (see Paris *et al.* 1981; Ferreti

et al. 1998). Trilobites clearly demonstrate climatic amelioration, with the Laurentian genus *Heliomera*, abundant odontopleurids, lichids and proetids (Hammann 1992; Hammann & Leone 1997), but mixed with taxa of Gondwanan origin such as calymenaceans. Bryozoan–cystoid reefs appeared at this time on the northern Gondwana platform (Vennin *et al.* 1998).

The polarward expansion of the low-latitude fauna is manifested also in the deep-water biota. The *Foliomena* Fauna first occurred in the early Late Ordovician in low latitudes (South China, Sibumasu), becoming widespread in the Sandbian and early Katian in deep-waters of temperate and tropical palaeocontinents (Baltica, Avalonia) and extending also to high latitudes (see Rong *et al.* 1999). In West Gondwana, the *Foliomena* fauna is known only from Sardinia (Villas *et al.* 2002) and Perunica; remaining areas of West Gondwana have extensive shallow shelves above the depth occupied by the *Foliomena* fauna. Palaeogeographical relationships of Perunica are thus obscured by differing lithologies and varied depth-related faunas. In Perunica, deep-water sites on outer shelves were first occupied by sparse faunas with *Chonetoidea* and *Cyclospira*, associated with abundant ostracodes and minute lingulaceans. *Dedzetina*, *Foliomena*, *Karlicium*, *Kozłowskites* and

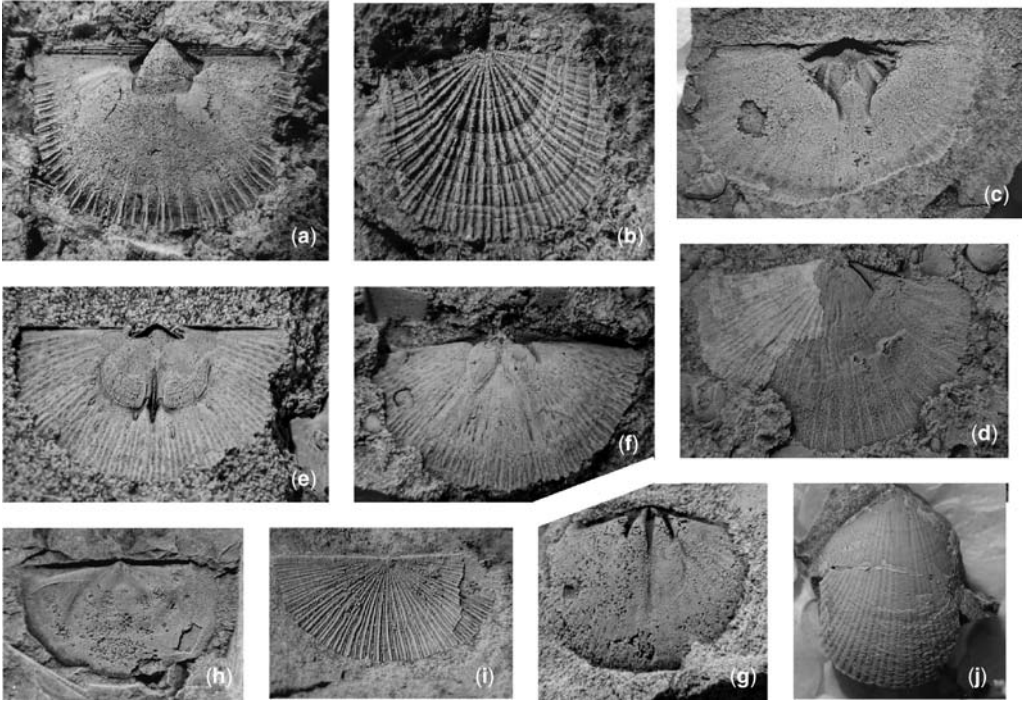


Fig. 14. Examples of endemic, Gondwanan, and cosmopolitan brachiopods of the Dapingian (**a, b**) Sandbian (**c–g**) and Katian (**h–j**) of Perunica. (**a, b**) endemic *Ferrax ooliticus*, PCZCU 1682, PCZCU 1683, LS = 9 mm, LS = 11 mm ventral valve and exterior of dorsal valve; (**c, d**) endemic *Blyskavomena blyskavense*, ventral and dorsal valves, PCZCU 1684, PCZCU 1685, LS = 9 mm, LS = 7 mm; (**e, f**) Gondwanan *Aegiromena praecursor*, ventral and dorsal valves PCZCU 1686, PCZCU 1687, LS = 6 mm, LS = 5 mm; (**g**) Gondwanan *Hirnatia kinneloides* PCZCU 1688, LS = 8 mm; (**h**) cosmopolitan *Foliomena folium*, PCZCU 1689, LS = 5 mm; (**i**) cosmopolitan *Chonetoides radiatula*, PCZCU 1690, LS = 3 mm; (**j**) endemic *Ornothyrella ornatella*, PCZCU 1691, LS = 11 mm. (**a, b**) Hlava, Klabava Formation; (**c–g**) Letná F., Loděnice; (**h–j**) Levín, Králův dvůr Formation.

Leptestiina appeared at about middle part of the Králův Dvůr Formation (Fig. 14); such taxa provide good correlation with the Boda event. The *Foliomena* fauna in the Prague Basin is less diverse, lacking *Christiana*, *Cyclospira*, *Sowerbyella* and other taxa known elsewhere (see Rong *et al.* 1999; Villas *et al.* 2002). Trilobites accompanying these small brachiopods constitute a typical atheloptic assemblage, with the trinucleid *Tretaspis anderssoni* and abundant, probably pelagic *Amphitryon*. Diverse cyclopygid trilobites are abundant (Marek 1961). Unlike in the earlier Ordovician, there are no records of a shallow-water fauna through almost the total thickness of the Králův Dvůr Formation, and comparison of the Perunica fauna with shallow shelf faunas of neighbouring terranes, including cratonic West Gondwana, is problematical. However, some links can be traced with the deep-water fauna of Baltica, because of the presence of *Tretaspis anderssoni*, a common species in the Oslo region and Poland. This similarity is probably

a result of climatic amelioration and spread of temperate fauna rather than palaeogeographical proximity of Perunica and Baltica, but some displacement of Perunica to lower latitude and towards Baltica cannot be excluded.

Near the top of the Králův Dvůr Formation, representing the latest Katian in the Prague Basin, there is a distinct lithological change (Štorch & Mergl 1989). A unique calcareous claystone has yielded an abundant and remarkably diverse benthic fauna (*Proboscisambon* Community; Havlíček 1982) containing the distinctly Gondwanan *Jezerzia*, a rare endemic *Boticium*, and with minute-sized and remarkably diverse small dalmanellids and plectambonitids (*Ravozetina*, *Salopina*, *Proboscisambon*, *Anoptambonites*, *Aegironetes* and *Kozłowskites*). Less common are brachiopods displaced from shallower sites (*Leptaena*, *Cliftonia*, *Cryptothyrella*, *Epitomyonia* and *Eoanastrophia*). Trilobites are richly diverse and very different from those in older beds; they include *Actinopeltis*,

Bojokoralaspis, *Decoroproetus*, *Dindymene*, *Duftonia*, *Gravicalymene*, *Marekolithus*, *Mucronaspis*, *Staurocephalus*, *Stenopareia* and *Zetaproetus*, but *Tretaspis*, *Amphitryon* and cyclopygids are already absent. Although this fauna is of distinctly deep-water character, it provides evidence of a warming event in Perunica. Common proetids, odontopleurids and other peculiar trilobites (*Phillipsinella*, *Trochurus*) are associated with abundant machaeridians, diverse ostracodes, bryozoans, cystoids and other echinoderms (*Mespilocystites*), a hyperstrophic gastropod *Mimospira*, and many other macroinvertebrates. The fauna contains many endemic species and can be considered as a stratigraphically younger and a somewhat deeper-water analogue of the *Nicolella* Fauna of SW Europe. The most diverse assemblages of this fauna in Perunica contain a higher proportion of shallow-water elements (large brachiopods, bivalves), occurring in the NE margin of the Ordovician deposits, indicating the presence of now eroded shallow-water deposits far toward the SE. The *Proboscisambon* Community fauna is the last manifestation of the Boda event in Perunica. The *Foliomena* Fauna reported from Sardinia (Villas *et al.* 2002) above the *Nicolella* Fauna shows some similarity to the *Proboscisambon* Community. In Sardinia, the *Foliomena* Fauna is associated with *Jezercia*, *Epitomomyonia* and *Skenidioides*, and is situated directly above the *Nicolella* Fauna and indicates a shoreward position (see Rong *et al.* 1999).

Climatic changes in the Hirnantian

Rapid climatic deterioration, sea-level fall and draining of the shallowest inshore areas drastically affected the fauna in Perunica and neighbouring terranes in the early Hirnantian. A low-diversity *Mucronaspis* Fauna appeared in the Prague Basin (Štorch & Mergl 1989), containing only *Mucronaspis*, *Duftonia* and a taxonomically poor associated fauna. This cool- or cold-water fauna is also known in other palaeocontinents, being reported from cratonic Gondwana, Baltica, South China and the margins of Laurentia (see Owen *et al.* 1991). However, the *Mucronaspis* Fauna is unknown in the ATA. In the Hirnantian the shallow shelves of the ATA were drained and karstification of the Katian limestones took place there. The appearance of the *Mucronaspis* Fauna in the Prague Basin is marked by an increase of bivalves and sudden and almost total disappearance of brachiopods. Hitherto undescribed minute *Disprosorthis* and *Fardenia* have been recorded. This sparse association is known also in marginal basins of Laurentia (Harper *et al.* 1994) and indicates that Perunica might have been situated in lower latitudes than could be deduced from the presence of diamictites just above the levels with the *Mucronaspis* Fauna. Sedimentation of diamictites had a fatal impact on the biota of Perunica and shelly faunas totally disappeared there (Štorch 1990; Brenchley *et al.* 1991).

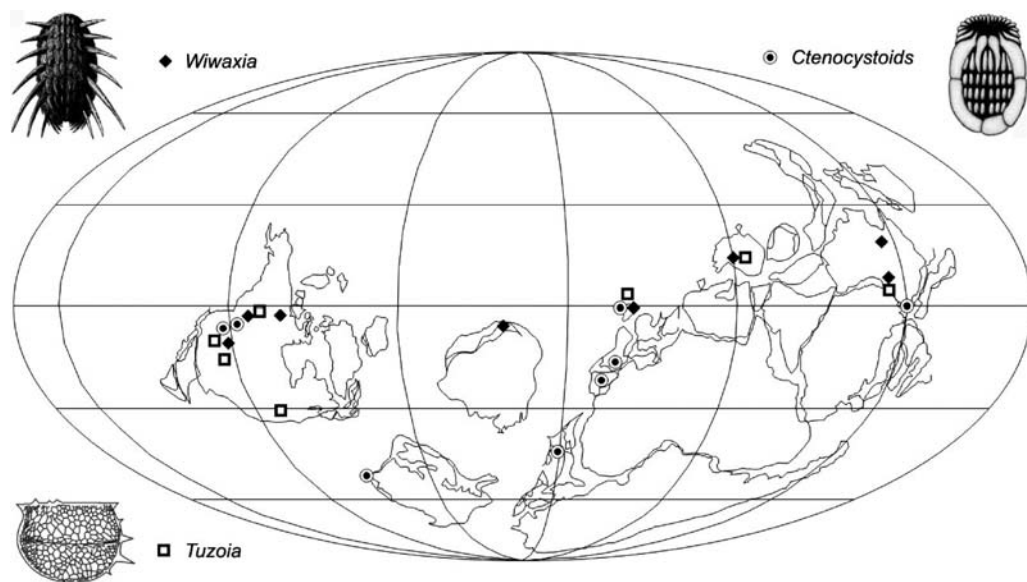


Fig. 15. Palaeogeographical distribution of the enigmatic genus *Wiwaxia*, ctenocystoid echinoderms and the bivalved crustacean genus *Tuzoia* in the 'early' and 'middle' Cambrian (adopted after McKerrow *et al.* 1994; Vannier *et al.* 2007; Fatka *et al.* 2009).

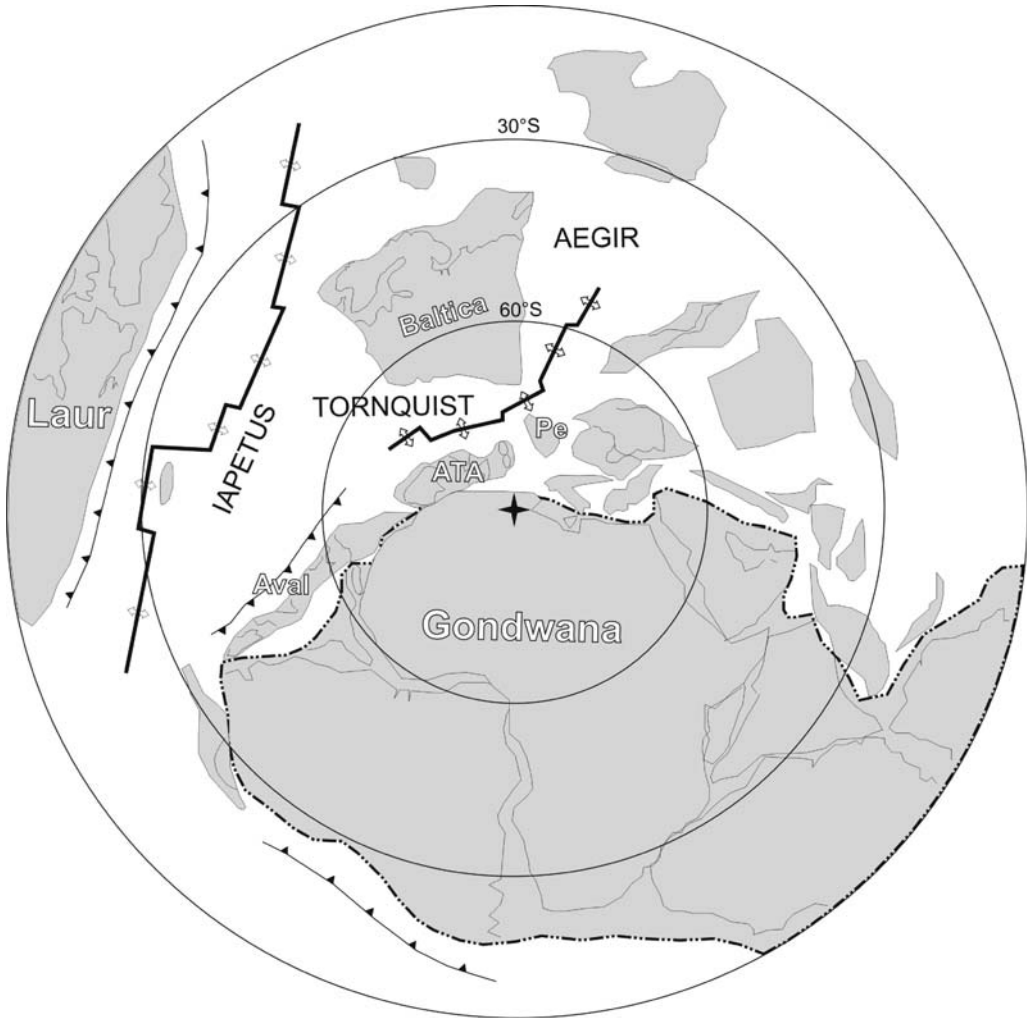


Fig. 16. Late Cambrian palaeogeographical reconstruction of the southern hemisphere modified from Cocks & Torsvik (2002, 2006). Laur, Laurentia; ATA, Armorican terrane assemblage; Aval, Avalonia; Pe, Perunica.

Recovery of the brachiopod-dominated fauna after melting of glaciers in the late Hirnantian is well documented in the Prague Basin (Štorch 1986). Inshore bivalve-dominated sandy beaches are followed by clayey sedimentation with a remarkably rich shelly fauna. Its composition and diversity is comparable with the rich *Hirnantia* fauna of the Kosov Province and is characteristic of the temperate zone, with the most common taxon being *Dalmanella testudinaria*. The fauna of Perunica is more diverse than the coeval poor fauna of the polar Bani province, which is reported from cratonic North African Gondwana and Armorica. Common taxa are *Hirnantia sagittifera*, associated with *Dalmanella*, *Comatopoma*, *Draborthis*,

Giraldibella, *Kinella*, *Ravozetina*, *Trucizetina*, *Cliftonia*, *Eostropheodonta*, *Leptaena*, *Leptaenopoma*, *Paromalomena*, *Plectothyrella*, *Zygospira*, *Philhedra*, *Sanxiaella*, large glossellids, bryozoans, gastropods, etc. Trilobites are represented by *Mucronaspis*, *Brongniartella* and *Bojokoralaspis*.

The *Hirnantia* Faunas marginal to Gondwana are less diversified than in Perunica. A poor fauna has been reported from western Brittany (Mélou 1987) and in the central Anti-Atlas in cratonic West Gondwana. Taxa include *Hirnantia*, *Arenorthis*, *Destombesium*, *Eostropheodonta*, *Plectothyrella* and *Undithyrella*. *Plectothyrella* is represented by *P. lybica* and *P. chauveli*, which differ from *Plectothyrella crassicosis* in Perunica.

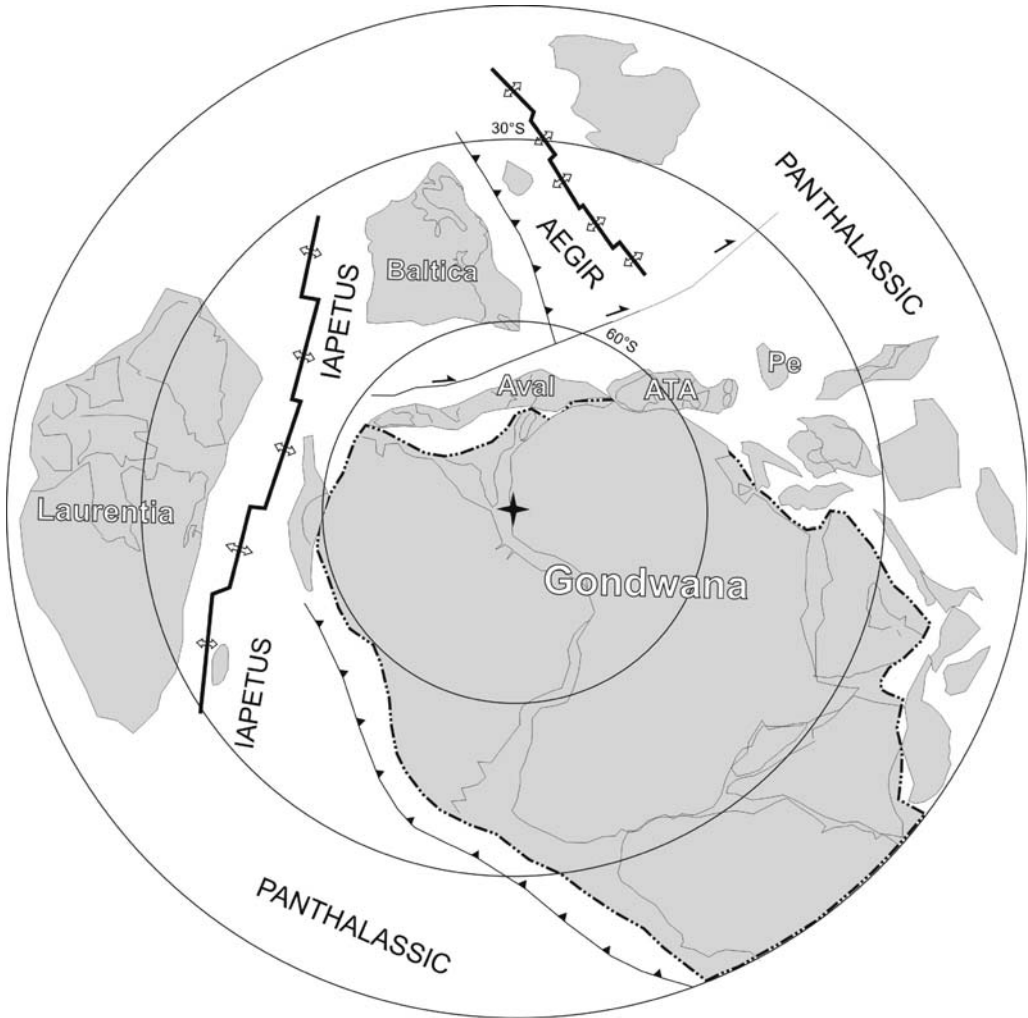


Fig. 17. Early Ordovician palaeogeographical reconstruction of the southern hemisphere modified from Cocks & Torsvik (2002, 2006).

P. crassicostis has been reported from other low-latitude palaeocontinents in the Hirnantian, including Baltica, Avalonia and marginal Laurentia. This led Havlíček (1990) to suggest a fairly temperate climatic position of Perunica in the Hirnantian, contrasting with the more boreal position of cratonic Gondwana and Armorica.

Northward shift of Perunica to low latitudes of the temperate zone, probably starting in the Katian, is evident from the composition of Llandoverey (Aeronian) benthic faunas in the Prague Basin (see Štorch 2001). Besides trilobites, in which proetids, harpids, scutellids, lichids and odontopleurids predominate, favositid corals and brachiopods with a significant proportion of plectambonitids,

strophomenids, rhynchonellids and atrypids appear. With these brachiopod groups some descendants of the Boda event are also present. *Jezercia*, *Saukrodictya*, *Epitomyonia*, *Hirnantia*, *Aegironetes* and *Proboscisambon* occur together with *Skenidioides*, *Dicoelosia*, *Dolerorthis* and *Stricklandia*. An offshore setting of this remarkable fauna is accentuated by the presence of the lingulate *Paterula*.

Conclusions

Perunica, as with a majority of other small independent terranes, experienced a dramatic paleogeographical history through the Late Precambrian and

Early Palaeozoic. Analyses of palaeontological content of the Cambrian and Ordovician sequences, combined with palaeomagnetic data, provide coherent datasets for possible positioning of Perunica during this time interval. Such analyses are biased by various factors, but recent evaluation of echinoderm, trilobite and brachiopod assemblages has provided a coherent picture of their distribution within inshore–offshore transects, which can be used reliably for restoration of palaeogeographical positions of the region.

In generally accepted reconstructions, the location of Perunica in very low (peri-equatorial) paleolatitudes during the ‘early–middle’ Cambrian times is clear (Fig. 15). This was followed by very

rapid displacement of the terrane to higher, peri-polar, latitudes during the late Cambrian (Fig. 16) and early Ordovician (Fig. 17). Such a European peri-Gondwanan story was constrained by the shift and rotation of the whole Gondwanan supercontinent in the southern hemisphere (Figs 16–18). Most areas with trilobite-bearing rocks of the Bohemian Massif were characterized by a gradual transfer from high polar paleolatitudes in the Late Ordovician (Fig. 18), through the cold and warm temperate belts during the Silurian to subtropical and tropical environments in the Devonian and Carboniferous, respectively. These changes had a crucial paleoenvironmental impact on the composition of trilobite assemblages that developed in this region.



Fig. 18. Latest Ordovician–earliest Silurian palaeogeographical reconstruction of the southern hemisphere modified from Cocks & Torsvik (2002, 2006).

The palaeogeographical path of Perunica traces a shift from tropical to subtropical climate in the 'early' Cambrian to a temperate 'middle' Cambrian, which was followed by transfer to a cooler climate in 'late' Cambrian to Middle and early Late Ordovician times. The absence of Cambrian and Early Ordovician carbonates is consistent with the high input of various but commonly weathered terrigenous material (as laterites).

Transgressive–regressive cycles make it possible to separate several depth-related assemblages in the Cambrian fauna of Perunica (Fatka *et al.* 2007). It is clear that shallower assemblages of agnostids can be classified as 'Mediterranean' and the deeper assemblages as 'Baltic' *sensu* Sdzuy (1972). Consequently, it is not possible to use such bathymetrically related forms for palaeogeographical interpretation. However, the tropical to subtropical position of Perunica is clearly indicated by the presence of climatically related taxa such as *Wiwaxia*, *Tuzoia* and ctenocystid echinoderms (Vannier *et al.* 2007; Fatka *et al.* 2009; Fig. 15). The absence of 'late' Cambrian faunas combined with shallow-water Tremadocian faunas minimizes any documentation of the following rapid shift to cooler latitudes. However, the comparatively warmest Ordovician climate was in the Floian and Dapingian, when diversity of invertebrates was remarkably high and some groups show a close relationship with Baltica. Climatic deterioration took place via a southward shift of Perunica from the Darriwilian. The generally cold-water character of Darriwilian assemblages is limited by the absence of shallow-water well-oxygenated facies in the basin mainly during Darriwilian and Katian times. The expansion of high-latitude Gondwanan faunas on siliciclastic shoals of Perunica and the generally deeper sedimentary regime with occasional dysaerobic conditions was characteristic until the Late Ordovician. Perunica appeared to be at about 60°S in the Middle Ordovician, but from that time a polarward path was reversed and Perunica began to move northwards. In the Katian, similar faunas to those of Baltica were related to position in a more or less comparable climatic belt and not be geographical proximity. As in other peri-Gondwanan sites, the Boda event led to the immigration of new faunal elements to Perunica. Despite the high-latitude position of Perunica in the Middle and early Late Ordovician, the new immigrants persisted until the drastic cooling at the beginning of the Hirnantian. Rapid melting of the ice sheet by the end of the Hirnantian brought a rich Hirnantian Fauna to Perunica shelves, including bryozoans, odontopleurid trilobites and gastropods. This rich fauna indicates relatively warmer climatic conditions compared with the poorer, more boreal Hirnantian Fauna of other parts of the

ATA (e.g. Armorica *s.s.*) and North Africa. This is consistent with movement of Perunica northwards, probably to 50–40°S latitude. A rise of sea level then brought anoxia to Perunica and terminated the expansion of the Hirnantian Fauna. From the beginning of the Silurian, Perunica was flooded by anoxic seas and only some shoals on submarine volcanic elevations allowed the persistence of rich benthic faunas. Corals and rich brachiopod faunas of Llandovery age indicate a mild to subtropical climate, consistent with the continuous shift of Perunica toward the Equator.

In general our analyses are in close agreement with Cocks & Torsvik (2002, 2006), but our data do not show any considerable distance from other segments of the ATA (Figs 16–18). Such a scenario is also consistent with the Nd–Sr–Pb isotopic record for Neoproterozoic to early Palaeozoic rocks of Perunica (Drost *et al.* 2004, 2007).

We are particularly grateful to Petr Kraft and Petr Budil (Prague) for helpful discussions. We would like to express our thanks to Mike Bassett (Cardiff) for reviewing and commenting on the manuscript. The Geological Society of London made it possible to participate in the Lyell Meeting in 2007. This research was supported by the Czech Science Foundation through the projects number 205/06/0395 and 205/09/1521.

References

- ÁLVARO, J. J. & VIZCAÍNO, D. 2000. Nouvel assemblage de trilobites dans le Cambrien moyen de la nappe de Pardailhan (Montagne Noire, France): implications biostratigraphiques dans la région méditerranéenne. *Eclogae Geologicae Helvetiae*, **93**, 277–289.
- BABIN, C. 1993. Role des plates-formes gondwaniennes dans les diversifications des mollusques bivalves durant l'Ordovicien. *Bulletin de la Société Géologique de France*, **164**, 141–153.
- BACHTADSE, V., TORSVIK, T. H., TAIT, J. A. & SOFEL, H. C. 1995. Paleomagnetic constraints on the paleogeographic evolution of Europe during the Paleozoic. In: DALLMEYER, R. D., FRANKE, W. & WEBER, K. (eds) *Pre-Permian Geology of Central and Eastern Europe*. Springer, Berlin, 567–578.
- BASSETT, M. G., POPOV, L. E. & HOLMER, L. E. 1999. Organophosphatic brachiopods: patterns of biodiversity and extinction on the early Palaeozoic. *Geobios*, **32**, 145–163.
- BASSETT, M. G., POPOV, L. E. & HOLMER, L. E. 2002. Brachiopods: Cambrian–Tremadoc precursors to Ordovician radiation events. In: CRAME, J. A. & OWEN, A. W. (eds) *Palaeobiogeography and Biodiversity Change: The Ordovician and Mesozoic–Cenozoic Radiations*. Geological Society, London, Special Publications, **194**, 13–23.
- BEDNARCZYK, W. 1964. The stratigraphy and fauna of the Tremadocian and Arenigian, Oelandian, in the Kielce region of the Holy Cross Mountains, Middle Poland. *Biuletyn geologiczny*, **4**, 3–216.

- BENEDETTO, J. L. 2007. New Upper Cambrian–Tremadoc rhynchonelliformean brachiopods from northwestern Argentina: evolutionary trends and early diversification of plectrothoideans in the Andean Gondwana. *Journal of Paleontology*, **81**, 261–285.
- BOUCOT, A. J., RONG, J.-Y., CHEN, X. & SCOTSESE, C. R. 2003. Pre-Hirnantian Ashgill climatically warm event in the Mediterranean region. *Lethaia*, **36**, 119–132.
- BRENCHLEY, P. J. & ŠTORCH, P. 1989. Environmental changes in the Hirnantian (Upper Ordovician) of the Prague Basin, Czechoslovakia. *Geological Journal*, **24**, 165–181.
- BRENCHLEY, P. J., ROMANO, M., YOUNG, P. Y. & ŠTORCH, P. 1991. Hirnantian glaciomarine diamictites—evidence for the spread of glaciation and its effect on Upper Ordovician faunas. In: BARNES, C. R. & WILLIAMS, S. H. (eds) *Advances in Ordovician Geology*. Geological Survey of Canada Papers, **90-9**, 325–336.
- BROCKE, R., FATKA, O., MOLYNEUX, S. G. & SERVAIS, T. 1995. First appearance data of selected Early Ordovician acritarch taxa from Peri-Gondwana. In: COOPER, J. D., DROSER, M. L. & FINNEY, S. C. (eds) *Ordovician Odyssey: Short Papers for the 7th International Symposium on the Ordovician System*. The Pacific Section Society for Sedimentary Geology (SEMP), Fullerton, 473–476.
- BROCKE, R., FATKA, O. & SERVAIS, T. 1998. A review of the Ordovician acritarchs *Aureotesta* and *Marrocanium*. *Annales de la Société Géologique de Belgique*, **120**, 1–21.
- BUSCHMANN, B., ELICKI, O. & JONAS, P. 2006. The Cadomian unconformity in the Saxo-Thuringian Zone, Germany: Palaeogeographic affinities of Ediacaran (terminal Neoproterozoic) and Cambrian strata. *Precambrian Research*, **147**, 387–403.
- CHÁB, J. 1978. Tentative lithostratigraphic and lithologic terminology for the Upper Proterozoic of the Teplá–Barrandian region. *Věstník Ústředního ústavu geologického*, **53**, 43–60 [in Czech].
- CHÁB, J. & PELC, Z. 1968. Lithology of Upper Proterozoic in the NW limb of the Barrandian area. *Krystalinikum*, **6**, 141–167.
- CHÁB, J. & PELC, Z. 1973. Proterozoic greywackes of the NW part of the Barrandian area. *Sborník geologických věd, Geologie*, **25**, 7–84.
- CHLUPÁČ, I. 1965. Xiphosuran Merostomes from the Bohemian Ordovician. *Sborník geologických věd, Paleontologie*, **5**, 7–38.
- CHLUPÁČ, I. 1995. Lower Cambrian arthropods from the Paseky Shale (Barrandian area, Czech Republic). *Journal of the Czech Geological Society*, **40**, 9–36.
- CHLUPÁČ, I. 1999a. Barrande's stratigraphic concepts, palaeontological localities and tradition—comparison with the present state. *Journal of the Czech Geological Society*, **44**, 3–30.
- CHLUPÁČ, I. 1999b. Unusual arthropods from the Bohemian Ordovician—a review. *Acta Universitatis Carolinae, Geologica*, **43**, 393–396.
- CHLUPÁČ, I. & HAVLÍČEK, V. 1965. *Kodymirus* n. g., a new aglaspid merostome of the Cambrian of Bohemia. *Sborník geologických věd*, **6**, 7–20.
- CHLUPÁČ, I., KRAFT, J. & KRAFT, P. 1996. Geology of fossil sites with the oldest Bohemian fauna (Lower Cambrian, Barrandian area). *Journal of the Czech Geological Society*, **40**, 1–8.
- CHLUPÁČ, I., HAVLÍČEK, V., KRÍŽ, J., KUKAL, Z. & ŠTORCH, P. 1998. *Palaeozoic of the Barrandian*. Český geologický ústav Praha.
- COCKS, L. R. M. 2000. The Early Palaeozoic of Europe. *Journal of the Geological Society, London*, **157**, 1–10.
- COCKS, L. R. M. 2002. Key Lower Palaeozoic faunas from near the Trans-European Suture Zone. In: WINCHESTER, J. A., PHARAOH, T. C. & VERNIERS, J. (eds) *Palaeozoic amalgamation of Central Europe*. Geological Society, London, Special Publications, **201**, 37–46.
- COCKS, L. R. M. & FORTEY, R. A. 1982. Faunal evidence for oceanic separations in the Palaeozoic of Britain. *Journal of the Geological Society, London*, **139**, 465–478.
- COCKS, L. R. M. & FORTEY, R. A. 1988. Lower Palaeozoic facies and fauna around Gondwana. In: AUDLEY-CHARLES, M. G. & HALLAM, A. (eds) *Gondwana and Tethys*. Geological Society, London, Special Publications, **37**, 183–200.
- COCKS, L. R. M. & FORTEY, R. A. 1990. Biogeography of Ordovician and Silurian faunas. In: MCKERROW, W. S. & SCOTSESE, C. R. (eds) *Palaeozoic Palaeogeography and Biogeography*. Geological Society, London, Memoirs, **12**, 97–104.
- COCKS, L. R. M. & FORTEY, R. A. 1998. The Lower Palaeozoic margins of Baltica. *GFF*, **120**, 173–179.
- COCKS, L. R. M. & LOCKLEY, M. G. 1981. Reassessment of the Ordovician brachiopods from the Budleigh Salterton Pebble Bed, Devon. *Bulletin of the British Museum (Natural History), Geology*, **35**, 111–124.
- COCKS, L. R. M. & TORSVIK, T. H. 2002. Earth geography from 500 to 400 million years ago: a faunal and palaeomagnetic review. *Journal of Geological Society, London*, **159**, 631–644.
- COCKS, L. R. M. & TORSVIK, T. H. 2005. Baltica from the late Precambrian to mid-Palaeozoic times: the gain and loss of a terrane's identity. *Earth-Science Reviews*, **72**, 39–66.
- COCKS, L. R. M. & TORSVIK, T. H. 2006. European geography in a global context from the Vendian to the end of Palaeozoic. In: GEE, D. D. & STEPHENSON, R. A. (eds) *European Lithosphere Dynamics*. Geological Society, London, Memoirs, **32**, 83–95.
- COCKS, L. R. M. & TORSVIK, T. H. 2007. Siberia, the wandering north terrane, and its changing geography through the Palaeozoic. *Earth-Science Reviews*, **82**, 29–74.
- COCKS, L. R. M., MCKERROW, W. S. & VAN STAAL, C. R. 1997. The margins of Avalonia. *Geological Magazine*, **134**, 627–636.
- COURTESOLE, R. & PILLET, J. 1978. La faune des couches à *Shumardia* du Tremadocien supérieur de la Montagne Noire. *Bulletin de la Société d'Historique Naturelle de Toulouse*, **114**, 176–186.
- DEAN, W. T. 1966. The lower Ordovician stratigraphy and trilobites of the Landeyran Valley and the

- neighbouring district of the Montagne Noire, south-western France. *Bulletin of the British Museum (Natural History), Geology*, **12**, 247–353.
- DESTOMBES, J., SOUGY, J. & WILLEFERT, S. 1969. Révisions et découvertes paléontologiques (Brachiopodes, Trilobites et Graptolites) dans le Cambre-ordovicien du Zemmour (Mauritanie septentrionale). *Bulletin de la Société Géologique de France, 7e Serie*, **11**, 185–206.
- DÖRR, W., ZULAUF, G., FIALA, J., FRANKE, W. & VEJNAR, Z. 2002. Neoproterozoic to Early Cambrian history of an active plate margin in the Teplá–Barrandian unit—a correlation of U–Pb isotopic dilution-TIMS ages (Bohemia, Czech Republic). *Tectonophysics*, **352**, 65–85.
- DROST, K., LINNEMANN, U. *ET AL.* 2004. New data on the Neoproterozoic–Cambrian geotectonic setting of the Teplá–Barrandian volcano-sedimentary successions: geochemistry, U–Pb zircon ages, and provenance (Bohemian Massif, Czech Republic). *International Journal of Earth Science (Geologische Rundschau)*, **93**, 742–757.
- DROST, K., ROMER, R. L., LINNEMANN, U., FATKA, O., KRAFT, P. & MAREK, J. 2007. Nd–Sr–Pb isotopic record of Neoproterozoic – Early Paleozoic siliciclastic rocks of the Barrandian (Bohemian Massif, Czech Republic). In: LINNEMANN, U., NANCE, D. R., KRAFT, P. & ZULAUF, G. (eds) *The Evolution of the Rheic Ocean: From Avalonian–Cadomian Active Margin to Alleghenian–Variscan Collision*. Geological Society of America, Special Papers, **423**, 191–208.
- DUFKA, P. & FATKA, O. 1993. Chitinozoans and acritarchs of the Ordovician–Silurian boundary from the Prague Basin (Barrandian area, Czechoslovakia). In: MOLYNEUX, S. G. & DORNING, K. J. (eds) *Contributions to Acritarchs and Chitinozoan Research*. Special Papers in Palaeontology, **48**, 7–16.
- DZIK, J. 1983. Early Ordovician conodonts from the Barrandian and Bohemian–Baltic faunal relationships. *Acta Palaeontologica Polonica*, **28**, 327–368.
- EGERQUIST, E. 2004. *Ordovician (Billingen and Volkhov stages) brachiopod faunas of the East Baltic*. Doctoral thesis, Uppsala University.
- ELICKI, O. & PILOLLA, G. L. 2004. Cambrian microfauna and palaeoecology of the Campo Pisano Formation at Gutturu Pala (Inglesiente, SW Sardinia, Italy). *Bollettino della Società Paleontologica Italiana*, **43**, 383–401.
- ELICKI, O., FATKA, O., GEYER, G. & ZYLINSKA, A. 2008. Cambrian. In: MCCANN, T. (ed.) *The Geology of Central Europe. Volume 1. Precambrian and Palaeozoic*. Geological Society, London, 153–202.
- FATKA, O. 1989. Acritarch assemblage in the *Onymagnos-tus hybridus* Zone (Jince Formation, Middle Cambrian, Czechoslovakia). *Věstník Ústředního Ústavu geologického*, **64**, 363–367.
- FATKA, O. 1990. Das Kambrium von Skryje und Týřovice. In: WEIDERT, K. H. (ed.) *Klassische Fundstellen der Paläontologie, Band 2*. Goldschneck, München, 12–17.
- FATKA, O. 1993. Chitinozoans and Acritarchs in latest Tremadoc–early Arenig sediments of the Prague Basin, Czechoslovakia. In: MOLYNEUX, S. G. & DORNING, K. J. (eds) *Contributions to Acritarchs and Chitinozoan Research*. Special Papers in Palaeontology, **48**, 29–36.
- FATKA, O. 2000. Das Mittlere Kambrium bei Jince, Tschechische Republik (Middle Cambrian at Jince, Czech Republic). In: PINNA, G. & MEISCHNER, D. (eds) *Europäische Fossilagerstätten*. Springer, Heidelberg, 21–23, 49–50, 244.
- FATKA, O. & BROCKE, R. 1999. Morphologic variability in two populations of *Arbusculidium filamentosum* (Vavrdová 1965) Vavrdová 1972. *Palynology*, **23**, 155–192.
- FATKA, O. & GABRIEL, Z. 1991. Microfossils from siliceous stromatolitic rocks of the Barrandian Proterozoic (Bohemian Massif). *Časopis pro Mineralogii a Geologii*, **36**, 143–148.
- FATKA, O. & KONZALOVÁ, M. 1996. Microfossils of the Paseky Shale (Lower Cambrian, Czech Republic). *Journal of the Czech Geological Society*, **40**, 55–66.
- FATKA, O. & PEK, I. 1999. Ordovician agnostid trilobites of the Prague Basin (Barrandian area, Czech Republic). *Acta Universitatis Carolinae, Geologica*, **43**, 381–384.
- FATKA, O., MOLYNEUX, S. G. & SERVAIS, T. 1997. The Ordovician acritarch *Frankea*: some critical remarks. *Geobios*, **30**, 321–326.
- FATKA, O., KORDULE, V. & SZABAD, M. 2004. Stratigraphic distribution of Cambrian fossils in the Příbram–Jince Basin (Barrandian area, Czech Republic). *Senckenbergiana Lethaea*, **84**, 369–384.
- FATKA, O., ŠINÁGL, M. & SZABAD, M. 2006. Mode of life of benthic suspension feeding echinoderms of the Middle Cambrian Jince Formation (Barrandian area, Czech Republic). In: LEFEBVRE, B., DAVID, B., NARDIN, E. & POTY, E. (eds) *Journees G. Ubahs, Programme and Abstracts, 17*. Biogeosciences, Université de Bourgogne, Dijon.
- FATKA, O., SZABAD, M. & VOKÁČ, V. 2007. Middle Cambrian associations of miomerid trilobites from Barrandian area (Czech Republic). In: ZLINSKÁ, A. (ed.) *8. paleontologická konference, Zborník abstraktov, Štátny geologický ústav Dionýza Štúra*, Bratislava, 32–34.
- FATKA, O., KRAFT, P. & SZABAD, M. *Wiwaxia* Walcott, 1911 in 'middle' Cambrian of the Barrandian area (Czech Republic). *Acta Palaeontologica Polonica* (In press).
- FERRETI, A., HAMMANN, W. & LEONE, F. 1998. Conodonts and biofacies from the Late Ordovician of Canamenda (Bacu Abis). *Giornale di Geologia*, **60**, Special Issue, 178–187.
- FORTEY, R. A. 1975. Early Ordovician trilobite communities. *Fossils and Strata*, **4**, 339–360.
- FORTEY, R. A. & COCKS, L. R. M. 2003. Palaeontological evidence bearing on global Ordovician–Silurian continental reconstructions. *Earth-Science Reviews*, **61**, 245–307.
- FORTEY, R. A. & COCKS, L. R. M. 2005. Late Ordovician global warming—the Boda Event. *Geology*, **33**, 405–408.
- FORTEY, R. A. & OWENS, R. M. 1978. Early Ordovician (Arenig) stratigraphy and fauna of the Carmarthen district, south-west Wales. *Bulletin of the British Museum (Natural History), Geology*, **30**, 225–294.

- FORTEY, R. A. & OWENS, R. M. 1987. The Arenig Series in South Wales: Stratigraphy and Palaeontology. *Bulletin of the British Museum (Natural History), Geology*, **41**, 169–307.
- FRANKE, W. 1989. Variscan plate tectonics in Central Europe—current ideas and open questions. *Tectonophysics*, **169**, 221–228.
- FRANKE, W. 2000. The mid-European segment of the Variscides: tectonostratigraphic units, terrane boundaries and plate tectonic extensions. In: FRANKE, W., ALTHERR, R., HAAK, V., ONCKEN, O. & TANNER, D. (eds) *Orogenic Processes: Quantification and Modelling in the Variscan Belt*. Geological Society, London, Special Publications, **179**, 35–66.
- GORJANSKY, V. J. 1969. *Inarticulate Brachiopods of Cambrian and Ordovician deposits of northwest of Russian platform*. Ministerstvo geologii RSFSR, Severo-zapadnoje territorialnyje geologičeskoe upravlenie, **6**, 3–176 [in Russian].
- GOZALO, R., LIÑAN, E. & ÁLVARO, J. 1994. Trilobites de la Subfamilia Solenopleurpsinae Thorai, 1947 del Cámbrico Medio de la Unidad de Alconera (Zona de Ossa Morena, SO de España). *Bolletín de la Real Sociedad Española de Historia Natural*, **89**, 43–54.
- GUTIÉRREZ-MARCO, J. C. & RABANO, I. 1987. Paleobiogeographical aspects of the Ordovician Mediterranean faunas. *Geogaceta*, **2**, 24–26.
- GUTIÉRREZ-MARCO, J. C., ALBANI, E. ET AL. 1996. Biostratigrafía de la Formación Pizarras del Sueve (Ordovícico Medio) en el sector septentrional de la escama de Laviana-Sueve (Zona Cantábrica, Norte de España). *Revista Española de Paleontología*, **11**, 48–74.
- GUTIÉRREZ-MARCO, J. C., RABANO, I. ET AL. 1999. Faunal dynamics between Iberia and Bohemia during the Oretanian and Dobrotivian (late Middle–earliest Upper Ordovician), and biogeographic relations with Avalonia and Baltica. *Acta Universitatis Carolinae, Geologica*, **43**, 487–490.
- HAMMANN, W. 1974. Phacopina und Cheirurina aus dem Ordovizium von Spanien. *Senckenbergiana Lethaea*, **55**, 151.
- HAMMANN, W. 1992. The Ordovician trilobites from the Iberian Chains in the Province of Aragon, NE Spain. I. The trilobites of the Cystoid Limestone (Ashgill Series). *Beringeria*, **6**, 1–219.
- HAMMANN, W. & LEONE, F. 1997. Trilobites of the post-Sardic (Upper Ordovician) sequence of southern Sardinia. Part I. *Beringeria*, **20**, 1–217.
- HAMMANN, W., ROBARDET, M. & ROMANO, K. 1982. *The Ordovician System in southwestern Europe (France, Spain, and Portugal)*. International Union of Geological Sciences Publication, **11**, 1–47.
- HARPER, D. A. T., MITCHELL, W. I. & RONG, J.-Y. 1994. New faunal data from the highest Ordovician rocks at Pomeroy, County Tyrone, Northern Ireland. *Scottish Journal of Geology*, **30**, 187–190.
- HAVLÍČEK, V. 1949a. Orthoidea a Clitambonoidea z českého tremadoku. *Sborník Státního geologického Ústavu Československé Republiky, Oddíl paleontologický*, **16**, 93–144.
- HAVLÍČEK, V. 1949b. Zpráva o geologickém mapování na Jinecku. *Věstník Ústředního ústavu geologického*, **25**, 98–103.
- HAVLÍČEK, V. 1968. The oldest macrofaunal horizon on Czechoslovak territory. *Časopis pro Mineralogii a geologii*, **13**, 211–212 [in Czech].
- HAVLÍČEK, V. 1970. *Pompeckium* and *Jamesella* (Orthacea, Brachiopoda) in the Middle Cambrian of Bohemia. *Věstník Ústředního ústavu geologického*, **45**, 289–290.
- HAVLÍČEK, V. 1971a. Stratigraphy of the Cambrian of Central Bohemia. *Sborník geologických Věd, Geologie*, **20**, 7–52.
- HAVLÍČEK, V. 1971b. *Brachiopodes de l'Ordovicien du Maroc*. Notes et Mémoires du Service Géologie du Maroc, **230**, 1–135.
- HAVLÍČEK, V. 1976. Evolution of Ordovician brachiopod communities in the Mediterranean province. In: BASSETT, M. G. (ed.) *The Ordovician System: Proceedings of a Palaeontological Association Symposium, Birmingham*. University of Wales Press and National Museum of Wales, Cardiff, 349–358.
- HAVLÍČEK, V. 1977. Brachiopods of the order Orthida in Czechoslovakia. *Rozpravy Ústředního Ústavu geologického*, **44**, 1–327.
- HAVLÍČEK, V. 1981. Upper Ordovician brachiopods from the Montagne Noire. *Palaeontographica, Abt. A*, **176**, 1–34.
- HAVLÍČEK, V. 1982. Ordovician of Bohemia: development of the Prague Basin and its benthic communities. *Sborník geologických věd, Geologie*, **37**, 103–136.
- HAVLÍČEK, V. 1989. Climatic changes and development of benthic communities through the Mediterranean Ordovician. *Sborník geologických věd, Geologie*, **44**, 79–116.
- HAVLÍČEK, V. 1990. Mediterranean and Malvinokaffric Provinces: new data on the Upper Ordovician and Lower Silurian brachiopods. *Časopis pro mineralogii a geologii*, **35**, 1–13.
- HAVLÍČEK, V. 1998. Ordovician. In: CHLUPÁČ, I., HAVLÍČEK, V., KRŽÍ, J., KUKAL, Z. & ŠTORCH, P. (eds) *Palaeozoic of the Barrandian*. Český geologický ústav, Praha, 149–164.
- HAVLÍČEK, V. 1999. Perunica microplate: relation to Ukrainian Shield, mid-Bohemian rift, and hypothetical large-scale overthrusts in central Bohemia. *Věstník Českého geologického ústavu*, **74**, 75–81.
- HAVLÍČEK, V. & BRANISA, L. 1980. Ordovician brachiopods of Bolivia. *Rozpravy České Akademie Věd*, **90**, 1–54.
- HAVLÍČEK, V. & JOSOPAIT, V. 1972. Articulate brachiopods from the Iberian Chains, Northern Spain (Middle Cambrian–Upper Cambrian–Tremadoc). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **140**, 328–353.
- HAVLÍČEK, V. & MAREK, L. 1973. Bohemian Ordovician and its international correlation. *Časopis pro Mineralogii a geologii*, **18**, 225–232.
- HAVLÍČEK, V. & ŠNAJDR, M. 1951. Cambrian and Ordovician at Jince and at the Brdy Hills. *Sborník Ústředního Ústavu geologického, oddíl geologický*, **18**, 145–276 [in Czech].
- HAVLÍČEK, V. & VANĚK, J. 1990. Ordovician invertebrate communities in black-shale lithofacies (Prague Basin, Czechoslovakia). *Věstník Ústředního ústavu geologického*, **65**, 223–236.

- HAVLÍČEK, V. & VANĚK, J. 1996. Dobrotivian/Berounian boundary interval in the Prague Basin with a special emphasis on the deepest part of the trough (Ordovician, Czech Republic). *Věstník Českého geologického ústavu*, **71**, 225–243.
- HAVLÍČEK, V., KRÍŽ, J. & SERPAGLI, E. 1987. Upper Ordovician Brachiopod Assemblages of the Carnic Alps, Middle Carinthia and Sardinia. *Bollettino della Società Paleontologica Italiana*, **25**, 277–311.
- HAVLÍČEK, V., VANĚK, J. & FATKA, O. 1994. Perunica microcontinent in the Ordovician (its position within the Mediterranean Province, series division, benthic and pelagic associations). *Sborník geologických věd, Geologie*, **46**, 23–56.
- KEPPIE, J. D., NANCE, R. D., MURPHY, J. B. & DOSTAL, J. 2003. Tethyan, Mediterranean, and Pacific analogues for the Neoproterozoic–Paleozoic birth and development of peri-Gondwanan terranes and their transfer to Laurentia and Laurussia. *Tectonophysics*, **365**, 195–219.
- KONZALOVÁ, M. 1981. Some late Precambrian microfossils from the Bohemian Massif and their correlation. *Precambrian Research*, **15**, 4–62.
- KRS, M. & PRUNER, P. 1999. To the palaeomagnetic investigations of palaeogeography of the Barrandian terrane, Bohemian Massif. *Acta Universitatis Carolinae, Geologica*, **43**, 519–522.
- KRS, M., KRŠOVÁ, M., PRUNER, P., CHOJKA, R. & HAVLÍČEK, V. 1986a. Paleomagnetism, paleogeography and multicomponent analysis of Middle and Upper Cambrian rocks of the Barrandian in the Bohemian Massif. *Tectonophysics*, **139**, 1–20.
- KRS, M., KRŠOVÁ, M., PRUNER, P. & HAVLÍČEK, V. 1986b. Paleomagnetism, palaeogeography and multicomponent analysis of magnetization of Ordovician rocks of the Barrandian area of the Bohemian Massif. *Sborník geologických věd, Užitá geofyzika*, **20**, 9–45.
- KUKAL, Z. 1971. Sedimentology of Cambrian deposits of the Barrandian area. *Sborník geologických věd, Geologie*, **20**, 53–100.
- KUKAL, Z. 1996. The Lower Cambrian Paseky Shale: Sedimentology. *Journal of the Czech Geological Society*, **40**, 67–78.
- LANDING, E. 2005. Early Paleozoic Avalon–Gondwana unity: an obituary—response to 'Palaeontological evidence bearing on global Ordovician–Silurian continental reconstructions' by R. A. FORTEY & L. R. M. COCKS. *Earth-Science Reviews*, **69**, 169–175.
- LEONE, F., HAMMANN, W., LASKE, R., SERPAGLI, E. & VILLAS, E. 1991. Lithostratigraphic units and biostratigraphy of the post-sardic Ordovician sequence in south-west Sardinia. *Bollettino della Società Paleontologica Italiana*, **30**, 201–235.
- LINNEMANN, U. & ROMER, R. L. 2002. The Cadomian Orogeny in Saxo-Thuringia, German: geochemical, and Nd–Sr–Pb isotopic characterisation of marginal basis with constraints to geotectonic setting and provenance. *Tectonophysics*, **352**, 33–64.
- MALETZ, J., STEINER, M. & FATKA, O. 2005. Middle Cambrian pterobranchs and the Question: what is a graptolite. *Lethaia*, **38**, 73–85.
- MAREK, L. 1961. The trilobite family Cyclopygidae Raymond in the Ordovician of Bohemia. *Rozprava Ústředního ústavu geologického*, **28**, 1–84.
- MATTE, P. 2001. The Variscan collage and orogeny (480–290 Ma) and the tectonic definition of the Armorica microplate: a review. *Terra Nova*, **13**, 122–128.
- MATTE, P., MALUSKI, H., RAJLICH, P. & FRANKE, W. 1990. Terrane boundaries in the Bohemian Massif: results of large-scale Variscan shearing. *Tectonophysics*, **177**, 151–170.
- McKERRROW, W. S., SCOTese, C. R. & BRASIER, M. D. 1992. Early Cambrian continental reconstructions. *Journal of the Geological Society, London*, **149**, 599–606.
- MÉLOU, M. 1987. Découverte de *Hirnantia sagittifera* (M'Coy, 1851) (Orthida, Brachiopoda) dans l'Ordovicien supérieur (Ashgillien) de l'extrémité occidentale du Massif Armoricain. *Geobios*, **20**, 679–685.
- MÉLOU, M. 1990. Brachiopodes articulés de la coupe de l'île de Rosan (Crozon, Finistère). Formation des Tufs et Calcaires de Rosan (Caradoc–Ashgill). *Geobios*, **23**, 539–579.
- MÉLOU, M., OULEBSIR, L. & PARIS, F. 1999. Brachiopodes et chitinozoaires Ordoviens dans le NE du Sahara Algérien: implications stratigraphiques et paléogéographiques. *Geobios*, **32**, 823–839.
- MERGL, M. 1983. New brachiopods (Cambrian–Ordovician) from Algeria and Morocco (Mediterranean Province). *Časopis pro mineralogii a geologii*, **28**, 337–348.
- MERGL, M. 1999. Genus *Paterula* (Brachiopoda) on Ordovician–Silurian sequence of Central Bohemia. *Věstník Českého geologického ústavu*, **74**, 347–361.
- MERGL, M. 2002. Linguliformean and craniiformean brachiopods of the Ordovician (Třenice to Dobrotivá Formations) of the Barrandian, Bohemia. *Acta Musei Nationalis Pragae, serie B, Historia Naturalis*, **58**, 1–82.
- MERGL, M. 2004. The earliest brachiopod–bryozoan dominated community in the Ordovician of peri-Gondwana and its ancestors: a case study from the Klabava Formation (Arenigian) of the Barrandian, Bohemia. *Journal of the Czech Geological Society*, **49**, 127–136.
- MERGL, M., GEYER, G. & EL ATARI, E. 1998. The billingsellid genus *Saccogonum* (Brachiopoda) from the Moroccan Cambrian and its significance for the regional geology and stratigraphy. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **209**, 273–293.
- MERGL, M., FATKA, O. & BUDIL, P. 2007. Lower and early Middle Ordovician trilobite associations of the Prague Basin (Perunica, Czech Republic). *Acta Paleontologica Sinica*, **46**, 320–327.
- MIKULÁŠ, R. 1996. Trace fossils from the Paseky Shale (Early Cambrian, Czech Republic). *Journal of the Czech Geological Society*, **40**, 37–54.
- MOCZYDŁOWSKA, M. 1999. The Lower–Middle Cambrian boundary recognized by acritarchs in Baltica and at the margin of Gondwana. *Bollettino della Società Paleontologica Italiana*, **38**, 207–225.
- NYSÄETHER, E., TORSVIK, T. H., FEIST, R., WALDERHAUG, H. J. & EIDE, E. A. 2002. Ordovician palaeogeography with new palaeomagnetic data from the Montagne Noire (Southern France). *Earth and Planetary Science Letters*, **203**, 329–341.

- OWEN, A. W., HARPER, D. A. T. & RONG, J. 1991. Hirnantian trilobites and brachiopods in space and time. In: BARNES, C. R. & WILLIAMS, S. H. (eds) *Ordovician Geology*. Geological Survey of Canada Paper, **90**, 179–190.
- PARIS, F. 1990. The Ordovician chitinozoan biozones of the Northern Gondwana Domain. *Review of Palaeobotany and Palynology*, **66**, 181–209.
- PARIS, F. & MERGL, M. 1984. Arenigian chitinozoans from the Klabava Formation, Bohemia. *Review of Palaeobotany and Palynology*, **43**, 33–65.
- PARIS, F., PELHATE, A. & WEYENT, M. 1981. Conodontes ashgilliens dans la Formation de Rosan coupe de Lostmarch (Finistère, Massif armoricain). Conséquences paléogéographiques. *Bulletin de la Société Géologique et Minéralogique de Bretagne*, **13**, 15–35.
- PHARAOH, T. C. 1999. Palaeozoic terranes and their lithospheric boundaries within the Trans-European Suture Zone (TESZ): a review. *Tectonophysics*, **314**, 17–41.
- POPOV, L. & HOLMER, L. E. 1994. Cambrian–Ordovician lingulate brachiopods from Scandinavia, Kazakhstan, and South Ural Mountains. *Fossils and Strata*, **35**, 1–156.
- POPOV, L. E., KHAZANOVITCH, K. K., BOROVKO, N. G., SERGEEVA, S. P. & SOBOLEVSKAYA, R. F. 1989. The key sections and stratigraphy of the phosphate-bearing *Obolus* Beds on the north-east of Russian Platform. *Nauka*, **18**, 5–222 [in Russian].
- POPOV, L. E., VINN, O. & NIKITA, O. I. 2001. Brachiopods of the redefined family Tritoechiidae from the Ordovician of Kazakhstan and South Urals. *Geobios*, **34**, 131–155.
- POPOV, L. E., EBBESTAD, J. O. R., MAMBETOV, A. & APAYAROV, F. K. 2007. A low diversity shallow water lingulid brachiopod–gastropod association from the Upper Ordovician of Kyrgyz Range. *Acta Palaeontologica Polonica*, **52**, 27–40.
- ROBARDET, M. 2003. The Armorica ‘microplate’: factor fiction? Critical review of the concept and contradictory palaeobiogeographical data. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **195**, 125–148.
- ROBARDET, M. & GUTIÉRREZ-MARCO, J. C. 2004. The Ordovician, Silurian and Devonian sedimentary rocks of the Ossa–Morena Zone (SW Iberian Peninsula, Spain). *Journal of Iberian Geology*, **30**, 73–92.
- RONG, J., ZHAN, R. & HARPER, D. A. T. 1999. Late Ordovician (Caradoc–Ashgill) brachiopod faunas with *Foliomena* based on data from China. *Palaios*, **14**, 412–431.
- SANCHEZ, T. M. & WAISFELD, B. G. 1995. Benthic assemblages in the Northwest of Gondwana: a test of the Ordovician evolutionary radiation model. In: COOPER, J. D., DROSER, M. L. & FINNEY, S. C. (eds) *Ordovician Odyssey*. The Pacific Section for Sedimentary Geology, Fullerton, CA, **77**, 409–412.
- SANCHEZ, T. M., CARRERA, M. G. & WAISFELD, B. G. 1999. Ordovician faunal turnover in the Argentine Pre-cordillera. *Acta Universitatis Carolinae, Geology*, **43**, 479–481.
- SCHÄTZ, M., REISCHMANN, T., TAIT, I., BACHTADSE, V., BAHLBURG, H. & MARTIN, U. 2002. The Early Palaeozoic break-up of northern Gondwana, new palaeomagnetic and geochronological data from the Saxothuringian Basin, Germany. *International Journal of Earth Science (Geologische Rundschau)*, **91**, 838–849.
- SDZUY, K. 1972. Das Kambrium der acadobaltischen Faunenprovinz. Gegenwärtiger Kenntnisstand und Probleme. *Zentralblatt für Geologie und Paläontologie, Teil II*, **1972**, 1–91.
- SDZUY, K. 2000. Das Kambrium des Frankenwaldes. 3. Die Lippertsgrüner Schichten und ihre Fauna. *Senckenbergiana Lethaea*, **79**, 301–327.
- SDZUY, K., HAMMANN, W. & VILLAS, E. 2001. The Upper Tremadoc fauna from Vogtendorf and the Bavarian Ordovician of the Frankenwald (Germany). *Senckenbergiana Lethaea*, **81**, 207–261.
- SERVAIS, T. & FATKA, O. 1997. Recognition of the Trans-European Suture Zone (TESZ) by the palaeobiogeographical distribution pattern of Early to Middle Ordovician acritarchs. *Geological Magazine*, **134**, 617–625.
- SERVAIS, T., BROCKE, R. & FATKA, O. 1996. Biometrics on *Dicrodiacrodium*: an example to document acritarch variability. *Palaeontology*, **39**, 389–405.
- SERVAIS, T., BROCKE, R., ERDTMANN, B. D. E., FATKA, O. & HEUSE, T. 2000. The importance of acritarchs in Ordovician biostratigraphy and palaeobiogeography in Germany. *Acta Universitatis Carolinae, Geologica*, **42**, 495–500.
- SMETANA, V. 1918. O některých gastropodech z kambria skrejsko-tejřovického. *Rozpravy české akademie věd a umění*, **27**, 1–13.
- ŠNAJDR, M. 1955. Trilobiti drabovských a letenských vrstev českého ordoviku. *Sborník Ústředního ústavu geologického, Oddíl paleontologický*, **22**, 477–533.
- ŠNAJDR, M. 1958. Bohemian Middle Cambrian trilobites. *Rozpravy Ústředního ústavu geologického*, **24**, 1–280 [in Czech with English summary].
- STEINER, M. & FATKA, O. 1996. Lower Cambrian tubular micro- to macrofossils from the Paseky Shales of the Barrandian area (Czech Republic). *Paläontologische Zeitschrift*, **70**, 275–299.
- ŠTORCH, P. 1986. Ordovician–Silurian boundary in the Prague Basin (Barrandian area, Bohemia). *Sborník geologických věd, Geologie*, **41**, 69–103.
- ŠTORCH, P. 1990. Upper Ordovician–lower Silurian sequences of the Bohemian Massif, central Europe. *Geological Magazine*, **127**, 225–239.
- ŠTORCH, P. 2001. Graptolite stratigraphy and depositional setting of the middle Llandovery (Silurian) volcanic–carbonate facies at Hýskov (Barrandian area, Czech Republic). *Věstník Českého geologického ústavu*, **76**, 55–76.
- ŠTORCH, P. & MERGL, M. 1989. Království–Kosov boundary and the late Ordovician environmental changes in the Prague Basin (Barrandian area, Bohemia). *Sborník geologických věd, Geologie*, **44**, 117–153.
- STOUGE, S. 2005. *Barrandeognathus* n. gen. (Conodonts) from the Komstad Limestone (lower Mid Ordovician), Scandinavia, and its palaeogeographical significance. *Bulletin of the Geological Society of Denmark*, **52**, 245–255.
- TAIT, J. A., BACHTADSE, V. & SOFFEL, H. C. 1994. New palaeomagnetic constraints on the position

- of central Bohemia during Early Ordovician times. *Geophysical Journal International*, **116**, 131–140.
- TAIT, J. A., BACHTADSE, V., FRANKE, W. & SOFFEL, H. C. 1997. Geodynamic evolution of the European Variscan fold belt: palaeomagnetic and geological constraints. *Geologische Rundschau*, **86**, 585–598.
- TORSVIK, T. H., SMETHURST, M., BRIDEN, J. C. & STURT, B. A. 1990. A review of Palaeozoic palaeomagnetic data from Europe and their palaeogeographical implications. In: MCKERROW, W. S. & SCOTSESE, C. R. (eds) *Palaeozoic Palaeogeography and Biogeography*. Geological Society, London, Memoirs, **12**, 25–41.
- TORSVIK, T. H., TRENCH, A., SVENSSON, I. & WALDERHAUG, H. J. 1993. Silurian palaeomagnetic results from Southern Britain: palaeogeographic significance and major revision of the Apparent Polar Wander Path for Eastern Avalonia. *Geophysical Journal International*, **113**, 651–668.
- TURVEY, S. T. 2002. Phylogeny of the Reedocalymeninae (Trilobita): implications for Early Ordovician biogeography of Gondwana. In: CRAME, J. A. & OWEN, A. W. (eds) *Palaeobiogeography and Biodiversity Change: The Ordovician and Mesozoic–Cenozoic Radiations*. Geological Society, London, Special Publications, **194**, 53–68.
- TURVEY, S. T. 2005. Reedocalymenine trilobites from the Ordovician of Central and Eastern Asia, and a review of species assigned to *Neseuretus*. *Palaeontology*, **48**, 549–575.
- URUNG, R., HARANCZYK, C. & CHOCYK-JAMINSKA, M. 1999. Easternmost Avalonian and Armorican–Caledonian terranes of Central Europe and Caledonian–Variscan evolution of the polydeformed Krakow mobile belt: geological constraints. *Tectonophysics*, **302**, 133–157.
- VAN DER VOO, R. 1979. Paleozoic assembly of Pangea: a new plate tectonic model for the Taconic, Caledonian and Hercynian orogenies. *EOS Transactions, American Geophysical Union*, **60**, 241.
- VANNIER, J., CARON, J. B., YUAN, J.-L., BRIGGS, D. E. G., COLLINS, D., ZHAO, Y.-L. & ZHU, M.-Y. 2007. *Tuzoia*: morphology and lifestyle of a large bivalved arthropod of the Cambrian seas. *Journal of Paleontology*, **81**, 445–471.
- VAVRDOVÁ, M. 1974a. Geographic differentiation of Ordovician acritarch assemblages in Europe. *Review of Palaeobotany and Palynology*, **18**, 171–176.
- VAVRDOVÁ, M. 1974b. Phytoplankton communities of Cambrian and Ordovician age of Central Bohemia. *Věstník Ústředního Ústavu geologického*, **57**, 145–155.
- VAVRDOVÁ, M. 1997. Early Ordovician provincialism in acritarch distribution. *Review of Palaeobotany and Palynology*, **98**, 33–40.
- VECOLI, M. & LE HÉRISSÉ, A. 2004. Biostratigraphy, taxonomic diversity and patterns of morphological evolution of Ordovician acritarchs (organic-walled microphytoplankton) from the northern Gondwana margin in relation to palaeoclimatic and palaeogeographic changes. *Earth-Science Reviews*, **67**, 267–311.
- VECOLI, M. & SAMUELSSON, J. 2001. Quantitative evaluation of microplankton palaeobiogeography in the Ordovician–Early Silurian of the northern Trans European Suture Zone: implications for the timing of the Avalonia–Baltica collision. *Review of Palaeobotany and Palynology*, **115**, 43–68.
- VENNIN, E., ALVARO, J. J. & VILLAS, E. 1998. High-latitude pelmatozoan–bryozoan mud-mounds from the late Ordovician northern Gondwana platform. *Geological Journal*, **33**, 121–140.
- VILLAS, E. 1985. Braquipedos del Ordovicio Medio y Superior de las Cadenas Ibericas Orientales. *Memorias del Museo Paleontologico de la Universidad de Zaragoza*, **1**, 1–153.
- VILLAS, E. 1992. New Caradoc brachiopods from the Iberian Chains (Northeastern Spain) and their stratigraphic significance. *Journal of Paleontology*, **66**, 772–793.
- VILLAS, E. 1995. Caradoc through Early Ashgill brachiopods from the Central-Iberian Zone (Central Spain). *Geobios*, **28**, 49–84.
- VILLAS, E., ARBIZU, M., BERNARDEZ, E., MENDEZ-BEDIA, I. & ARAMBURU, C. 1995. *Protambonites primigenius* (Brachiopoda, Clitambonitidina) y el límite Cámbrico-Ordovícico en la Serie de los Cabos (Zona Asturoccidental-Leonesa, NO de Espana). *Revista Española de Paleontología*, **10**, 140–150.
- VILLAS, E., HAMMANN, W. & HARPER, D. A. T. 2002. *Foliomena* Fauna (Brachiopoda) from the Upper Ordovician of Sardinia. *Palaeontology*, **45**, 267–295.
- WINCHESTER, J. A., PHARAOH, T. C. & VERNIERS, J. 2002. Palaeozoic amalgamation of Central Europe: an introduction and synthesis of new results from recent geological and geophysical investigations. In: WINCHESTER, J. A., PHARAOH, T. C. & VERNIERS, J. (eds) *Palaeozoic amalgamation of Central Europe*. Geological Society, London, Special Publications, **201**, 1–18.
- XU, H. & LIU, D. 1984. Late Lower Ordovician brachiopods of southwestern China. *Bulletin Nanjing Institute Geology and Palaeontology, Academia Sinica*, **8**, 147–237.
- ZULAUF, G. 1997. Von der Anchizone bis zue Eklogifazies: Angekippte Krustenprofile als Folge der Cadomischen und variscischen Orogenese im Teplá–Barrandium (Böhmische Masse). *Geotektonische Forschungen*, **89**, 1–302.
- ZULAUF, G., SCHITTER, F., RIEGLER, G., FINGER, F., FIALA, J. & VEJNAR, Z. 1999. Age constraints on the Cadomian evolution of the Teplá–Barrandian unit (Bohemian Massif) through electronmicroprobe dating on metamorphic monazite. *Zeitschrift der Deutschen Geologischen Gesellschaft*, **150**, 627–639.