Distribution patterns of Upper Devonian phacopid trilobites: Paleobiogeographical and paleoenvironmental significance

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ABSTRACT

Phacopid trilobites are relatively widespread in Devonian deposits. After a maximum diversity in the Middle Devonian, most phacopids were severely affected by repeated sea-level eustatic changes, especially in the Frasnian and it was during that time that the main groups of reduced-eye or blind phacopids arose. The aim of this investigation was to evaluate the distribution patterns of Upper Devonian phacopids at a global level through a clustering analysis, in a paleogeographical and paleoenvironmental framework in order to understand their fluctuations in time and space. The phacopid biodiversity is represented in this study by 22 taxa from the Frasnian to the late Famennian. Additionally, four main time intervals (Frasnian I, Famennian Post-I, Famennian II–III, and Famennian IV–VI) have been explored. To complete the clustering analysis, two ordering methods, i.e. a seriation routine and a detrended correspondence analysis have been performed respectively to reveal chronological sequences and to identify indirect paleoenvironmental gradients. Analyses enabled us to establish (1) bathymetrical gradients showing some taxa such as Omegops restricted to shallower environments and other taxa such as Ductina or Dianops to deeper environments; and (2) paleobiogeographical affinities showing exchanges along the margins of North-Gondwana and Avalonia/Baltica and probable connections along the margin of North-East Gondwana, after the major mid-Givetian Taghanic transgression.

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1. Introduction

Trilobites were important elements of the Devonian macrobenthos and especially Phacopidae that were relatively abundant and diverse in marine Devonian habitats. They were present over a range from shallower to deeper environments (Crônier, 1999; Crônier and Courville, 2003). In particular, the Late Devonian was an important period for the development of phacopid trilobites because the main groups of reduced-eye or blind phacopids arose at that time, notably in the North-Peri-Gondwanian margin. These Upper Devonian phacopids are among the youngest representatives and have the fewest eyelenses (Crônier et al., 2011). Indeed, after a maximum development in diversity and number in the Middle Devonian, most phacopids that were adapted to the outer-shelf bottom habitats after the major mid-Givetian Taghanic transgression (Johnson, 1970), were severely affected by repeated sea-level rises, especially in the Frasnian (Feist, 1991; Crônier et al., 2013). Recently, an analysis of phacopid diversity has been carried out and different curves (diversity, origination and extinction) were constructed (Crônier et al., 2013) showing their dynamics throughout the Late Devonian. In the context of a deepening ocean, these Upper Devonian phacopids were subject to evolutionary changes such as the gradual reduction of the visual complex leading to blindness (Crônier and Courville, 2003; Crônier et al., 2004, 2011). The current knowledge of Upper Devonian trilobites has been widely documented since the pioneer works of Richter and Richter (1926, 1955) and the subsequent studies of Maksimova (1955), Osmólska (1958, 1963), Chlupáč (1966, 1977), Feist et al. (2009) and Crônier et al. (2013), among others.

The aim of this study is to assess the distribution patterns of Upper Devonian phacopids through clustering analysis in a paleogeographical and paleoenvironmental framework in order to understand their fluctuations in time and space. To complete the clustering analysis, a seriation routine and a detrended correspondence analysis have been performed respectively to reveal chronological sequences and to identify indirect paleoenvironmental gradients. Compositional changes and replacements in the phacopid assemblages throughout the Late Devonian are linked to paleoenvironmental fluctuations, influenced by global events.

2. Material and methods

2.1. Sampling

We focused investigations on samples from Upper Devonian strata, mostly obtained from the published data, in order to examine and to model the distribution patterns of phacopid assemblages at a global level. The phacopid biodiversity is represented in this study by 22 taxa, i.e. 18 phacopid genera (or subgenera) plus four poorly assigned taxa (consideration of ‘granulatus’ group and ‘cryphoides’ taxon
(Crônier et al., 2013); a distinction is made between Phacops sensu lato from the Frasnian and the Famennian; see Table 1 for the taxonomic list) for 31 geographical areas. The taxonomic status of some phacopid taxa remains problematic (McKellar and Chatterton, 2009; Crônier et al., 2011). For example, the ‘granulatulus’ group from the Late Devonian differs (especially by its distinctive L1 without intercalating ring, a less developed visual complex, a shorter (sag) pygidium and a lighter tuberculation) from the ‘Phacops’ sensu lato group. The study of their relationship and their alpha-taxonomy is still in progress (by Crônier and Holloway); we will therefore use ‘Phacops sensu lato’ for Upper Devonian species with a developed visual complex and a distinction between Phacops sensu lato from the Frasnian and the Famennian is adopted.

Additionally, four main time intervals including: 15 geographical areas and six taxa for the Frasnian I interval; 7 geographical areas and two taxa for the Famennian Post-I, interval, 18 areas and nine taxa for the Famennian II and III intervals and 24 areas and seven taxa for the Famennian IV to VI intervals have been explored. I to VI refer to successive Frasnian–Famennian cephalopod zones (Wedekind, 1908).

2.2. Distribution of paleoprovinces/paleocommunities through three time intervals

In order to understand the distribution patterns of Upper Devonian phacopids, an attempt to analyze associations and faunal gradients has been undertaken. This analysis based on the presence/absence of taxa is regarded as preliminary before taking into account the total number (or relative abundance) of specimens in similar facies in future studies. The term association is used here for recurrent assemblages of trilobites with similar taxonomic composition (Chlupáč, 1987; Brenchley and Harper, 1998; Thomas and Lane, 1999; Crônier and van Viersen, 2007).

The trilobite database was analyzed with a hierarchical cluster analysis. This approach is commonly applied to palaeoecological problems (Cugny, 1988; Brenchley and Harper, 1998; Botakuil and Racheboeuf, 2010), especially on Cambro–Ordovician trilobites (Ludvigsen and Westrop, 1983; Balseiro et al., 2010; Hughes and Thomas, 2011), and helped in the identification of discrete associations.

Clustering analysis is an exploratory and agglomerative technique that groups together commonly recurring samples and/or taxa by level of similarity (Davis, 1986; Harper, 1999; Hammer and Harper, 2006). Results of Q-mode clustering, with its columns of samples, and R-mode clustering, with its columns of taxa, are presented as dendrograms, which were achieved using the paired-group algorithm and the correlation using the Rho similarity measure (Hammer and Harper, 2006). Groups of taxa with a high probability of co-occurrence are thus grouped together. Hierarchical cluster analysis was performed at the generic level because the data treatment at the species level is often inadequate for taxonomic purposes (Hallam, 1977; Cecca, 2002).

Hierarchical cluster analysis was carried out on the presence/absence of 22 taxa to display mainly co-occurrence of trilobites especially for the Late Devonian, but also for four main studied time intervals, i.e. Frasnian I, Famennian Post-I, Famennian II–III and Famennian IV–VI through the Late Devonian. This procedure gives equal importance to all taxa and minimizes the effect of highly abundant ones for well-known sections; and it allows integration of data from literature. Additionally, an analysis of similarities (ANOSIM) that is a non-parametric test was achieved for statistically significant differences between groups of taxa and for the comparison of their taxonomic composition (Clarke, 1993; Hammer and Harper, 2006).

2.3. Faunal and paleoenvironmental gradients through four time intervals

To complete the clustering analyses and to obtain an ordering of taxa and deposits, we used a seriation routine that is often used for reconstructing a chronological sequence. This method is applied to an association matrix with taxa in the rows and samples in the columns. The binary data are stored in an unsorted contingency table indicating, which taxa can be found in which sample. The seriation routine reorganizes the data matrix by rearranging the taxa and samples so that the presences are concentrated along the matrix diagonal. This method uses two algorithms described by Brower and Kyle (1988); a constrained and an unconstrained optimization.

In constrained optimization, the samples have a known order according to their stratigraphical level or their position along a presumed faunal gradient. To find the ‘optimal’ biozonation, only the taxa are freely reordered. The ordering of taxa may reveal a biostatigraphical sequence of overlapping taxon ranges. Additionally, the seriation routine runs a ‘Monte Carlo’ randomization (Tipper, 1980) that generates and seriates 30 random matrices (with the same number of occurrences within each taxon) in order to test whether the original matrix differs significantly from randomly seriated matrices and is more informative than these randomly seriated matrices.

In unconstrained optimization, both samples and taxa are freely reordered in order to concentrate the presences along the matrix diagonal. The corresponding ordering of both taxa and samples may reveal a biogeographical/environmental gradient or a stratigraphical sequence.

Finally, for an identification of indirect environmental gradients, we used a Detrended correspondence analysis (DCA). DCA is considered more reliable than any other factor analyses for ecological and paleoecological studies (Hammer et al., 2001; Holland et al., 2001) is a multivariate-based ordination technique commonly used on ‘ecological’ data sets to recognize and quantify environmental factors that may be influencing faunal distribution patterns (Hill and Gauch, 1980; Scarponi and Kowalewski, 2004; Bonelli and Patzkowski, 2008). DCA that maximizes the correspondence between taxa and samples and estimates the location of the peak abundance of taxa, provides ordination scores for both taxa and samples. DCA was achieved using the detrending procedure to avoid the arch effect of a traditional correspondence analysis in involving a compression of the total information along the first axis, which often reflects paleoenvironmental gradients (Hammer and Harper, 2006). Hierarchical cluster analyses, ANOSIM, seriations and detrended correspondence analyses were conducted using the data-analysis software PAST v2.08 (Hammer et al., 2001; Hammer and Harper, 2006).

Table 1

<table>
<thead>
<tr>
<th>Taxa</th>
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<tbody>
<tr>
<td>Aculicryphops Crônier and Feist, 2000</td>
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<tr>
<td>Babinops Feist and Becker, 1997</td>
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<tr>
<td>Cryptops Richter and Richter, 1926</td>
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<tr>
<td>Dianops Richter and Richter, 1923</td>
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<tr>
<td>Diemostus Richter and Richter, 1931</td>
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<tr>
<td>Durcima Richter and Richter, 1931</td>
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<tr>
<td>Eldredgesops Struve, 1950</td>
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<tr>
<td>Houseops Feist, McNamara, Crônier and Lerosey-Aubril, 2000 ['true' Houseops; from the Famennian]</td>
</tr>
<tr>
<td>Houseops(?) Feist, McNamara, Crônier and Lerosey-Aubril, 2009 [assignment uncertain; from the Frasnian]</td>
</tr>
<tr>
<td>H.? cryphoides Phillips and Richter, 1926</td>
</tr>
<tr>
<td>Nephropops Richter and Richter, 1926</td>
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<tr>
<td>Omopsops Struve, 1976</td>
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<tr>
<td>Phacops Eismirch, 1839 [distinction between Phacops sensu lato from the Frasnian and the Famennian]</td>
</tr>
<tr>
<td>Phacops sensu lato from the Frasnian and the Famennian</td>
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<tr>
<td>Group of P.I. granulatus Münster, 1840</td>
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<tr>
<td>Rhabidopsops Struve, 1989</td>
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<tr>
<td>Spinicryphops Crônier and Feist, 2000</td>
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<tr>
<td>Struzeugops Crônier and Feist, 2000</td>
</tr>
<tr>
<td>Trimerocephaloides Feist, McNamara, Crônier and Lerosey-Aubril, 2009</td>
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<tr>
<td>Trimerocephalus McCoy, 1849</td>
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<tr>
<td>Trimerocephalus (Trilobops) Crônier, 2003</td>
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<tr>
<td>Weyerites Crônier and Feist, 2000</td>
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3. Paleoassociative, paleoenvironnemental and paleobiogeographical results

3.1. Paleocommunities and paleoassociative interpretation

A first hierarchical cluster analysis performed on the presence/absence of 22 taxa for the Late Devonian shows three occurrences and four clusters (Fig. 1). Some current geographical areas are characterized by their endemic and/or poorly known fauna: Northeast America with only the endemic Frasnian genus Eldredgeops, Northwest Australia with its endemic genera Trimerocerphaloides (Frasnian) and Babinops (Famennian), the Urals with the poorly known Frasnian Houseops? and East Asia, Altai and South France with the poorly known Phacops s.l. from the Frasnian.

Others geographical areas are characterized by a rich and diverse fauna. Germany (Rhenish Massif, Thurinia, Harz Mts.), Turkey and Spain are characterized by the common Frasnian Acuticryphops and common or numerous Famennian II–III taxa (Trimerocerphalus, Ductina). Current Central and Western Europe (Poland, Franconia, Silesia, Austria and Central–east and Northwest France corresponding to the paleogeographical South Laurussia margin, i.e. the South European margin of the Old Red Sandstone continent and the Gondwana-derived European Hunic terrane margins) and North Africa (corresponding to the paleogeographical North Peri-Gondwanan margin) are characterized by Famennian IV–VI taxa such as Dianops or Weyerites. Finally, current Central and Western Europe (Moravia, Northeast France/Southwest Belgium and England), North Africa (Morocco), South and North China, Southwest Russia, Afghanistan and Iran along the paleogeographical Paleotethys ocean margins are characterized by late Famennian taxa such as Omegops.

However, in order to better understand faunal associations through the Late Devonian, a second hierarchical cluster analysis was performed on presence–absence data for four main time intervals. This second analysis shows four superclusters and two non-clustering occurrences that can be interpreted as temporal associations (Fig. 2). Supercluster 1 comprises genera from the Frasnian I; supercluster 2, genera from the Famennian Post-I o; supercluster 3, genera from the Famennian II and III; supercluster 4, genera from the Famennian IV to VI. Each non-clustering occurrence comprises only one genus from the Frasnian I. Through these temporal superclusters and non-clustering occurrences, five associations and five occurrences can be delineated (Fig. 2).

Three occurrences and one association come from the Frasnian I: (1) Eldredgeops occurrence (a non-clustering occurrence) encountered only in Northeast America: Eldredgeops that comes from the Givetian.
and persists into the Frasnian (C. Brett and J. Zambito, pers. comm.) occurs as the only genus present; (2) Houseops? occurrence (a non-clustering occurrence) encountered only in the Urals: Houseops? originated in the early Frasnian occurs as the only genus present; (3) Phacops s.l. occurrence encountered mainly in East Asia: two samples from Asia that lack other trilobites and two samples from Turkey and southwest France that include the mid-late Frasnian Acuticryphops; and (4) Acuticryphops association encountered mainly in the current Central and Western Europe (England, Rhenish Massif, Harz Mts, Moravia, Thuringia and Spain, i.e. the Avalonia superterrane and the European Hunic terranes), North Africa and northwest Australia. The ‘cryphoides’ taxon is randomly present in this association. Additionally, Acuticryphops is a pandemic taxon for this time.

Only one occurrence comes from the Famennian Post-Iδ: Nephranops occurrence. This occurrence encountered only in the current Central and Western Europe (Poland, Harz Mts, Franconia, Thuringia, Southwest France) occurs as the only genus present.

One occurrence and two associations come from the Famennian II–III: (6) Babinops occurrence encountered only in northwest Australia: Babinops occurs with Trimeroccephalus or Houseops in this area; (7) T. (Trifoliops) association encountered in the current Central and Western Europe (southwest France and Poland) and North Africa with Phacops s.l. in Algeria: samples are also characterized by the occurrence of Trimeroccephalus; and (8) Dactina association dominated by Dactina and Trimeroccephalus mainly in the current Central and Western Europe (i.e. in the Avalonia superterrane and the European Hunic terranes): Dactina is invariably present in this association while Trimeroccephalus is absent only in Central China. All other genera, i.e. Dienstina, Houseops, Cryphops and Struveops are randomly present in this association. Compared with all other associations, generic richness is highest here. Regarding Cryphops, this taxon seems to appear during the late Famennian Post-Iδ but it is more common in the Famennian II. Consequently, its occurrence has been taken into account only for the Famennian II and III for the seriation routine and the detrended correspondence analysis. Regarding Houseops, this taxon ‘reappeared’ after a pseudo-extinction around late Frasnian; however Houseops of the Frasnian are morphologically different from those of the Famennian, and probably represent two distinct genera (a distinction between Houseops? from the Frasinian I and the true Houseops from the Famennian II and III is made). Trimeroccephalus that is present in many samples except in Central China is a pandemic taxon for this time. The occurrence of Trimeroccephalus in the Ural Mountains during the Famennian IV–V is probably an error of dating. This occurrence has not been taken into account for the seriation routine and the detrended correspondence analysis.

And finally two associations come from the Famennian IV to VI. (9) Dianops association dominated by Dianops and Weyerites occurs mainly in the current Central and Western Europe: Dianops is invariably present in this association while Weyerites is present randomly. (10) Omegops association dominated by Omegops and the ‘granulatus’
taxon occurs mainly in the current Eurasia (England, Northeast France/Southwest Belgium, Iran, Afghanistan, Southwest Russia and China) along the both paleogeographical South Laurussia and North Peri-Gondwana margins: Omegops is invariably present in this association. The ‘granulatus’ taxon is a pandemic taxon for this time but it is absent in Northeast France/Southwest Belgium, Afghanistan and Southwest Russia.

ANOSIM was applied to test for the significant differences between the three identified superclusters and the non-clustering occurrence using 5000 permutations and a correlation measure. The R coefficient is respectively 0.8225 and the p value is < 0.0002, providing a significant differences between taxa groupings and supporting the results of the hierarchical cluster analysis.

3.2. Faunal gradient and paleoenvironmental interpretation

Because the taxa from the Frasnian I and the Famennian Post-Iδ are present randomly and often as single occurrences (two non-clustering occurrences on four and a single association), these two intervals are put together for the seriation routine and the detrended correspondence analysis.

The location of six taxa encountered during the Frasnian I plus Nephranops from the Famennian Post-Iδ, according to an unconstrained seriation routine (Fig. 3) seems to show a spatio-temporal distribution with the oldest genera to the east of the peri-Laurussian margin (Eldredgebys in the northeast of the North America, Houseops? in the Urals and Phacops s.l. mainly in East Asia) and the youngest genera to the north of the peri-Gondwanan margin (Acuticryphops and Nephranops in North Africa and the current Central and Western Europe and Trimeroccephaloids and Acuticryphops in Northwest Australia).

To complete the hierarchical clusters analysis and the seriation routine, a detrended correspondence analysis (DCA) was carried out on fossil occurrences. The major axis DC1 (not represented here) segregates three distinct faunas: two areas represented by a single taxon with Eldredgebys only in Northeast America and Houseops? only in the Urals against a third diversified area.

The two next axes (DC2–DC3) distribute all other samples along a gradient and seem to show a temporal environmental gradient correlating with water depth from shallower to deeper environments: from Phacops s.l. to H? cryphoides on the one hand, and from Phacops s.l. to Nephranops on the other hand (Fig. 4). High DC2-low DC3 scores correspond to shallower water taxa such as Phacops s.l., a well-developed-eye taxon, whereas low DC2-low DC3 or high DC2-high DC3 scores relates to deeper water taxa such as H? cryphoides, a reduced-eye taxon or Nephranops, a blind taxon.

For the Famennian II–III, the location of genera according to an unconstrained seriation routine (Fig. 5) seems to shows a spatio-temporal correspondence: between the current Central Europe (Rhenish Massif, Harz Mts and Thuringia, i.e. the Rhenohercynian and Saxothuringian zones) and the Urals with diversified taxa such as Ductina, Houseops, Cryphops, Struveops and Dienstina, on the one hand, and between the current North Africa/Central and Western Europe/Iran and Northeast China with only Trimeroccephalus on the other hand. Babinops occurs only in the north–western of Australia.

The results of DCA based on faunal contents are significant (eigenvalues = 0.9816 for DC1 and DC2) and seem to show a linear distribution of the samples along DC1 axis (Fig. 6). The majority of the information that is explained by DC1 axis (eigenvalues = 0.5999) can
be interpreted as a bathymetrical gradient from shallower to deeper environments. In this gradient, the *Ductina* association tends to be towards the deepest end (low DC1) and *Phacops s.l.* lies at the shallowest end (high DC1). In the same way, along DC2 axis (eigenvalues = 0.3817), the *Babinops* occurrence seems to lie at the shallowest end (high DC2).

For the Famennian IV to VI, the location of genera according to an unconstrained seriation routine seems to show a spatio-temporal evolution where the current Central and Western Europe appears to be the center of origin and/or rather the best studied area (Fig. 7). Moreover, there is a correspondence: (1) between Rhenohercynian domain/South China and the Urals with *Dianops*/'granulatus' and *Omegops*, (2) between Avalonia/North Africa/Iran and North China with *'granulatus'*/*Omegops*, and (3) between Rhenohercynian domain/Afghanistan and Southeast Russia with only *Omegops*.

The results of DCA based on faunal contents are significant (eigenvalues = 0.7263 for DC1 and DC2). The majority of the information is explained by DC1 axis (eigenvalues = 0.5041), which clearly reveals a main faunal gradient (Fig. 8). Scores of taxa show the tendency of fauna to co-occur and their alignment may reflect differentiation according to a main environmental factor correlative with water depth from deeper to shallower environments, i.e. from *Dianops*/Weyerites/Spinicryphops to *Omegops* through *'granulatus'*/Rabienops (Fig. 8). This interpretation is based on the occurrence of samples comprising *Omegops*, a well-developed-eye taxon from shallower water (high DC1 axis), and samples such as *Dianops* (blind taxon) or *Weyerites* (reduced-eye taxon) from deeper-water (low DC1 axis).

4. Paleoenvironmental and paleogeographical discussions and conclusions

4.1. Spatiotemporal distribution

This study represents the first detailed account of a phacopid-dominated bathymetrical gradient for the late Devonian time. The hierarchical cluster analysis performed on Upper Devonian phacopid taxa allows us to delineate five occurrences and five discrete phacopid associations from the early Frasnian to late Famennian reflecting their distinctive taxonomic affinities (Fig. 2). The distribution of these occurrences and associations is partly related to spatial/ecological gradients, for example, the *Dianops association* characterizes more distal...
environments while the Omegops association more proximal environments for the late Famennian; or temporal gradients, for example, the Dianops association replaces the Ductina association during the Famennian (Fig. 9). Trilobites that mostly belong to the vagrant epibenthos, living actively above the substrate where conditions are not homogeneous, were sensitive to paleoenvironmental fluctuations. Areas of the same environmental gradient are very similar to each other in the trilobite content, even if a faunal replacement seems to exist through time.

Trilobite associations are relatively precise paleoenvironmental indicators in recognizing marine environments of different depths and reflect some ecological conditions ranged across shelves (Fortey and Brett, 1986; Turvey, 2005; Crônier and van Viersen, 2007). Along a bathymetric profile (modified from Fortey and Owens, 1997; Brenchley and Harper, 1998), four main environments can be recognized: (1) the shoreface environment characterized by shallow, proximal and agitated deposits including trilobites as fragmented exoskeletons in sandstones; (2) the upper offshore or inner shelf environment characterized by mudstones intercalated with sandstones including trilobites as disarticulated and fragmented exoskeletons and/or as coquinas; (3) the median offshore or middle shelf environment characterized by relatively deep deposits including moderately to highly diverse assemblages with well-developed eye trilobites, clumped or dispersed sclerites commonly articulated in mudstones; and (4) the lower offshore or outer shelf environment located below effective storm wave-base including rare trilobites, as articulated exoskeletons, often blind or with reduced-eyes, in shales.

Consequently, the state of preservation and/or nature of sediment and the associated fauna known for some assemblages allow us to locate, at least approximately, fossil sites along such bathymetric profiles. Fig. 9 attempts to show the spatio-temporal evolution of the Upper Devonian phacopids.

Among the major recognized associations, the Acuticryphops association dominated by Acuticryphops, the most common reduced-eyed phacopid of the late Frasnian (a period characterized by a pronounced eustatic rise and rapid fluctuations in sea level — Girard et al., 2005), is mainly encountered in pelagic euxinic deposits, i.e. of lower offshore deposits (Fig. 9). The Nephranops occurrence (in the current Central and Western Europe, along the paleogeographical Rheno-Hercynian ocean margins) from the Post-l6 is encountered in micritic nodular limestones intercalated with argillites and anoxic black shales (Crônier, 2007; Feist et al., 2009) of lower offshore deposits (Fig. 9). The mixed Ductina association (mainly in the current Central and Western Europe, along the paleogeographical Rheno-Hercynian ocean margins) dominated by blind Ductina and Trimerocephalus and with randomly present reduced-eyed taxa (Dienstina, Houseops, Cryphops and Struverops) is concentrated rather in pelagic shaly limestones of the Famennian II and III (Chlupáč, 1975, 1977), probably of the upper part of lower offshore deposits or the lower part of median offshore deposits (Fig. 9). The Dianops association (mainly in the current Central and Western Europe) is dominated by blind Dianops and reduced-eyed Weyerites accompanied by taxa with well-developed eyes (‘granulatus’) and is concentrated rather in commonly nodular cephalopod limestones of the Famennian IV–VI (Chlupáč, 1966, 1975, 1977) characteristic for the upper part of the lower offshore deposits (Fig. 9). The Omegops association (known mainly in the current Eurasia, along the both paleogeographical South Laurussia and North Peri-Gondwanan margins) dominated by Omegops with well-developed eye and the ‘granulatus’ taxon is concentrated in shallow-water deposits influenced by current activity (previously reported by Chlupáč, 1975, 1977). This association is encountered in shallow water clastic limestones probably of lower shoreface to upper offshore origin during the late Famennian (Fig. 9).

4.2. Migration routes/exchanges

While some taxa are restricted to a specific area such as Eldredgeops, which is encountered only in North America during the basal Frasnian, other taxa are repeatedly reported or widely distributed. This is the case of Acuticryphops that characterizes the Frasnian, Trimerocephalus...
typical for the Famennian II–III or P. ‘granulatus’ for the Famennian IV–VI.

Frasnian phacopids show a significantly low taxonomic similarity, and a similar evolutionary pattern of eye-reduction from both the South European margin of the Old Red Sandstone Continent and the North peri-Gondwanan margin, supporting geographical connections between these areas and a worldwide eustatic deepening prior to the Late Kellwasser extinction Event (Feist, 2002). This exchange, already functional during the Middle Devonian corresponds to the evolution of the Old World Province (Chlupáč, 1975, 1994; McKellar and Chatterton, 2009) and of the Rheono-Hercynian domain involving the drifting northward of the European Hunic terranes accreted individually to Laurussia during the Variscan cycle (Raumer et al., 2003; Golonka and Gaweda, 2012).

As a consequence of the major Frasnian extinction, the basal Famennian is greatly depleted in trilobites. The blind Nephropsan, found in the Rheono-Hercynian domain and the European Hunic terranes (Richter and Richter, 1926; Becker et al., 1989) from black shales formed under anoxic conditions (Feist et al., 2009) is the earliest Famennian phacopid known, occurring as early as the Middle triangularis Zone (Becker and Schreiber, 1994; Feist and Schindler, 1994).

In the early Famennian, recuperation took place with the relatively rich and diverse Ductina association known for a long time from various European regions i.e. in the Avalonia superterrane and the European Hunic terranes (Richter and Richter, 1926, 1955; Osmólska, 1958, 1963; Chlupáč, 1966, 1977). The occurrence of the blind genus Trimeroccephalus along the South European margin of the Old Red Sandstone Continent between the Rhenish Slate Mountains and the Urals but extending also into North Africa (Alberti, 1970; Crônier and Feist, 1997; Crônier et al., 2013) suggests a faunal exchange along the western Paleotethys margin. Moreover, its presence in Australia demonstrates a possible faunal exchange along the northeastern Gondwanan margin (Feist et al., 2009). Despite the continued presence of blind genera (Ductina and Trimeroccephalus), the early Famennian was a time for the restoration of oculated phacopids such as observed in Australia with Houseops (Feist et al., 2009).

During the late Famennian, a relatively rich radiation of phacopids took place. As suggested by Chlupáč (1975) and Feist and Becker (1997), the distribution of late Famennian phacopids suggests a faunal exchange within the Old World Province between South Laurussia/ Avalonia-derived superterrane and European Hunic terrane margins, North-Africa (‘Maghrebo–European Realm’), South China and Asiatic Hunic terranes, and Central Asia along the margins of the Paleotethys ocean. Phacopid assemblages from South and North China described by Xiang (1981), Zhu (1988) and Yuan and Xiang (1998) also proved to be rather similar, despite the large longitudinal distance along the
margins of the Paleotethys ocean. Phacopid assemblages from Iran (Feist et al., 2003) also proved to be rather similar and constitute an important link between the faunas of the South European margin of the Old Red Sandstone continent/North Peri-Gondwanan margin toward the west and those of South China/Australia toward the east. Added to the continued presence of benthic trilobites, the migrations are also observed within nektonic organisms such as clymeniids during the late Famennian (Becker and Mapes, 2010). Additionally, clymeniids that occur in a black shale facies of southern North America (Oklahoma) similar to that from the hypoxic shales of the southern Morocco (Maider Basin) show a selective faunal exchange between southern North America and northern of North Africa in the uppermost Famennian (Becker and Mapes, 2010). By contrast, no Famennian phacopid trilobites are known from western Gondwana (i.e. South America) and North America prior to the latest Famennian Hangenberg Event that precipitated the extinction of all phacopids.

5. Conclusions

As stated above, this is the first detailed characterization of a phacopid-dominated bathymetrical gradient for the late Devonian time. Along this bathymetrical gradient, we recognized some taxa such as Omegops restricted to shallower environment and others taxa such as Ductina or Dianops to deeper environments, in accordance with previous assumptions (Chlupáč, 1975, 1977).

The distribution of some recognized associations, on the basis of presence/absence taxa, and their replacements are correlated with the global sea curve (from Johnson et al., 1985) and due to rapid alteration of the ecosystems related to a pronounced eustatic rise and rapid fluctuations in sea level. Some trends can be observed: 1) extension of extern platforms favoring an homogeneous habitat over a large epicontinental area (i.e. expansion of pelagic facies) along the margins of North-Gondwana and Avalonia/Baltica (Feist and Schindler, 1994; Haq and Schutter, 2008) resulting in a sub-cosmopolitism in phacopids after the major mid-Givetian Taghanic transgression (Johnson, 1970); 2) pronounced sea-level deepening in Devonian time (Johnson et al., 1985; Feist, 1991; Girard et al., 2005; Haq and Schutter, 2008) led to major morphological adaptations such as the reduced size and the gradual regression of the visual complex in various taxa adapted to life in deep-water habitats, i.e. ‘cephalopod biofacies’; 3) the rich and mixed Ductina (blind) association flourished during a period of sea-level high-stand and known from the median offshore to the upper part of lower offshore domain; and 4) the Omegops (oculated) dominated association spreads out during a phase of relative sea-level lowstand and is known from the lower shoreface to upper offshore domain.

During the Late Devonian, rapid regressive sea-level fluctuations of the end-Frasnian and of the end-Famennian (Johnson et al., 1985; Girard et al., 2005) led to major extinctions within the deep benthic communities. The Kellwasser extinction triggered the decline of phacopids (extinction of several important and well-diversified genera; see Crônièr et al., 2013). After a significant post-Kellwasser recovery during the late early Famennian leading to a major faunal turnover (see Crônièr et al., 2013) and the occurrence of new phacopid paleocommunities, the Hangenberg event caused the extinction of the, by now, strongly impoverished phacopid trilobites.

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Fig. 9. Localization of Upper Devonian phacopid assemblages through time and a bathymetric profile, and comparison with the global sea-level curve.

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