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Trilobite faunal dynamics on the Devonian continental shelves of the Ardenne Massif and Boulonnais (France, Belgium)

ARNAUD BIGNON and CATHERINE CRÔNIER



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During the Devonian the sedimentation on the continental shelves of Ardenne Massif and Boulonnais has changed from a mixed siliciclastic-carbonate ramp (Eifelian), through a carbonate barrier reef (Givetian) and then to a detrital influx with local mud-mounds (Frasnian). Here we analysed the faunistic dynamics of the trilobite associations through the changing environment. We used multivariate analyses (clustering and ordering) to discriminate the trilobite associations within 67 different samples. Three previously known communities and one new were recognised: the Eifelian Mixed association, the Givetian *Dechenella* association and the two Frasnian *Bradocryphaeus* and *Scutellum–Goldius* associations. These trilobite faunas present a progressive ecological specialisation. The Mixed association occurs both in the ramp or carbonated (local reef developed on the ramp) facies without any significant difference in its composition. The *Dechenella* fauna occurs preferentially close to barrier reefs, but can also survive during short periods of detrital input. The two Frasnian communities show a strong relationship with their environment. The *Scutellum–Goldius* association is only found in reef systems, whereas the *Bradocryphaeus* flourishes exclusively in lateral facies.

Key words: Trilobita, faunal succession, reefs, Devonian, France, Belgium, Ardenne Massif, Boulonnais.

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Introduction

The Ardenne Massif and the Boulonnais (northeast of France, Belgium) are classic areas to study the late Paleozoic reefal systems. The diversity of environments recorded in the Middle and Upper Devonian deposits of these regions allow to investigate relationships between the environmental changes on the continental shelf and the benthic biodiversity. The Eifelian mixed ramp turns into a carbonate platform during the Givetian (Boulvain et al. 2009), and then is drowned in the Frasnian leading to the development of carbonate mud mounds (Boulvain 2001). Such a series of environmental transformations provides a good opportunity to study the factors controlling the carbonate factory (Boulvain et al. 2009). The research on the trilobites from the Ardenne has been commenced by Mailleux (e.g., 1904, 1909, 1919, 1927, 1933, 1938) and subsequently continued by other researchers (e.g.,

Asselbergs 1912, 1946; Richter and Richter 1918, 1926). These early works revealed specific affinities with the Eifel fauna in Germany (Rhenohercynian area). After fifty years of relative disinterest, the more recent detailed works on Devonian trilobites of the Ardenne have shown that there is actually an important distinction between these areas at this taxonomic level (e.g., Magrean and van Viersen 2005; van Viersen 2006, 2007a, b; van Viersen and Prescher 2009, 2010; van Viersen and Bignon 2011; Bignon and Crônier 2011).

The Devonian biodiversity of Ardenne trilobites was previously analysed by Crônier and van Viersen (2007) through multivariate analyses. Three associations were identified in the Middle and Upper Devonian: the Mixed association characteristic for the Eifelian, the *Dechenella* and *Nyterops* association for the Givetian and the *Bradocryphaeus* association occurring in the middle Frasnian. These associations are well constrained temporally and appear to be controlled mainly by the palaeobathymetry.

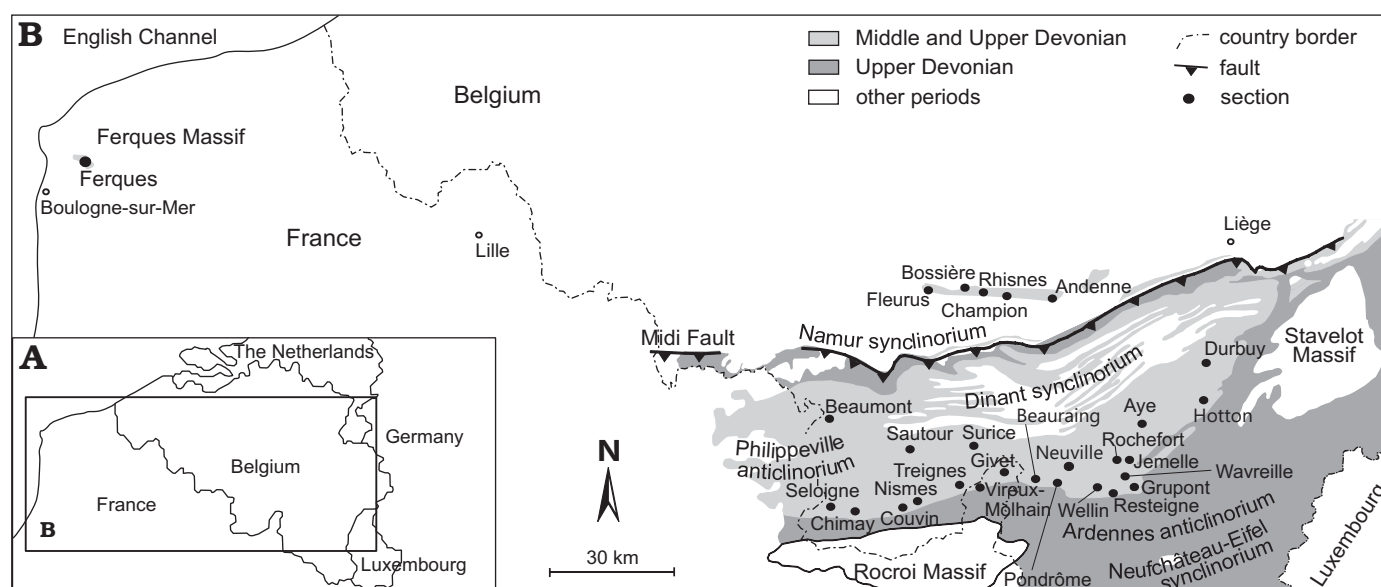


Fig. 1. Geographic location of the studied area (A) and geological map of the Ardenne and Boulonnais areas (B) with studied fossiliferous sections (modified after Crônier and van Viersen 2007).

The present work details the preliminary study of Crônier and van Viersen (2007). More than 20 new sections have been added to the original database offering a detailed sampling of the Ardenne Massif and a comparison with the Boulonnais. Moreover, the samples have been re-organised by formations or members. These lithostratigraphic units provide a shorter temporal constraint and a more accurate palaeoenvironmental framework than the substages used in the previous study. Unfortunately, the palaeoenvironmental conditions were not determined bed by bed (except for the Givet section), and we were not able to assess the variation occurring in the same lithological unit though such an information is considered whenever available. The aims of this study are (i) a description of distribution patterns of benthic communities during a reef ecosystem build-up and drowning and (ii) an evaluation of their distribution along the platform and their environmental tolerance.

Abbreviations.—ANOSIM, analysis of similarities; DCA, Detrended Correspondence Analysis; FWWB, Fair Weather Wave Base; HCA, Hierarchical Cluster Analysis; SWB, Storm Wave Base.

Geological setting

The Ardenne Massif (France–Belgium) corresponds to the western part of the Rhenohercynian area and follows structurally a WSW–ENE axis. The Midi fault delimits the south Ardenne allochthon overlapping the Brabant para-autochthon in the north (Mansy and Lacquement 2006). From south to north the allochthon is composed of Neufchâteau-Eifel synclinorium, Ardennes anticlinorium, Philippeville anticlinal, and Dinant synclinorium. The para-

autochthon is composed of Namur synclinorium and Brabant Massif (Fig. 1).

The Boulonnais (France) belonged to the eastern extremity of the Weald-Artois anticline (Fig. 1). The Devonian corresponds to the “Lower” Boulonnais of the Ferques Massif (Brice 1988).

After the Caledonian orogeny, the Ardenne Massif and Boulonnais constituted a passive margin boarding the southeastern part of the Old Red Sandstone continent (Averbuch et al. 2005). A siliciclastic material produced by the dismantling of the continent fed the basin from the North during the Lower Devonian. A sea-level increase (Johnson et al. 1985) led to the development of a mixed siliciclastic-carbonate ramp during the Eifelian (Ziegler 1982; McKerrow and Scotese 1990). This transgressive phase favoured the trilobite diversification reaching a peak in the Devonian (Crônier and van Viersen 2007). Locally, the ramp was associated with favourable environmental conditions allowing the erection of a reefal system corresponding to the Couvin Formation (Mabille and Boulvain 2007a). During the Eifelian–Givetian transition the extension of a sea-level rise led to the formation of a carbonate platform associated with a wide reef (Préat and Mamet 1989; Kasimi and Préat 1996). During the Frasnian, this platform was suddenly flooded and carbonated mud mounds settled in a deep mixed siliciclastic-carbonate ramp (Boulvain 2001).

A complete description of the Devonian formations from the Ardenne Massif was published by Bultynck and Dejonghe (2001). Boulvain et al. (1999) gave a particular focus to the Frasnian. Givetian and Frasnian formations of the Boulonnais were detailed in Brice and collaborators (1979) and Brice (1988). Stratigraphic relationships between these areas (Fig. 2) were described by Hubert (2008). The main characteristics of these lithostratigraphic units are summarised in the Table 1.

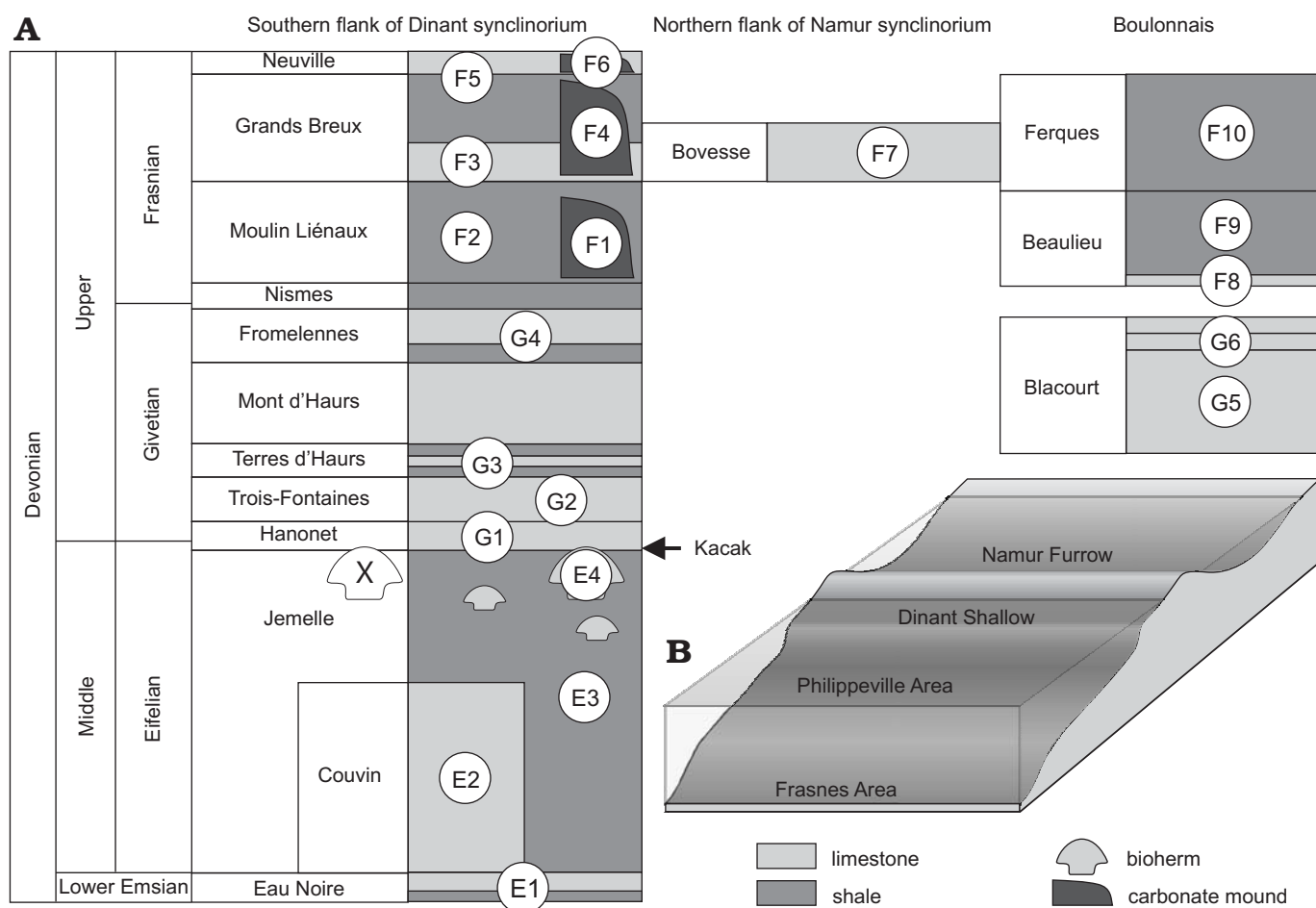


Fig. 2. Generalized lithostratigraphic section of Middle and Upper Devonian of the Ardenne Massif (France-Belgium) and Boulonnais (France) **A**. Correlation of the Ardenne Massif and Boulonnais formations. E1, Eau Noire Formation; E2, Couvin Formation; E3, Jemelle Formation; E4, X Formation; G1, Hanonet Formation; G2, Trois-Fontaines Formation; G3, Terres d'Haus Formation; G4, Fromelennes Formation; G5, Griset Member; G6, Couderousse Member; F1, Arche Member; F2, Ermitage Member; F3, Bieumont Member; F4, Lion Member; F5, Boussu-en-Fagne Member and Neuville Formation (lateral facies); F6, Neuville Formation, Petit Mont Member; F7, Bovesse Formation; F8, Noces Member; F9, Pâturage Member; F10, Ferques Formation (after Bultynck and Dejonghe 2001 and Hubert 2008). **B**. Reconstruction of the Frasnian platform of the Ardenne Massif (after Da Silva and Boulvain 2012).

Material

The previous database used by Crônier and van Viersen (2007) for Middle and Upper Devonian (around 700 specimens) has been completed with new data sampled in the field (more than 500 specimens; Bignon and Crônier 2011; van Viersen and Bignon 2011), literature and the Maillieux collection (2000 trilobites; e.g., Maillieux 1909, 1927, 1933, 1938), housed in the Institut Royal des Sciences Naturelles de Belgique, Belgium. Thus 21 sections belonging to the southern flank of the Dinant synclinorium, and five to the Namur synclinorium, where the Devonian outcrops are the most fossiliferous in the Ardenne Massif (Hubert et al. 2007), were analysed in this study (Fig. 1). Additionally, another section representing the Boulonnais was included in the new database, adding around 50 specimens originating from sampling and collection (Morzadec 1988; Morzadec et al. 2007) of the Université Catholique de Lille, France (SOM 1: Table S1 in Supplementary Online Material available at http://app.pan.pl/SOM/app60-Bignon_Cronier_SOM.pdf). Because the data are of

multiple origins (museum collection, literature, field sampling), only the relative abundance of taxa has been analysed here in order to reduce sampling bias as suggested by Harnik (2009). Indeed, the number of specimens and taxonomic richness in a section are strongly influenced by sampling effort (Thompson 2004). Thus, the relative abundance seems to be a better reflection of the biodiversity (SOM 2: Table S2).

The count includes large fragments, complete and disarticulated specimens. Free cheeks, thoracic segments, and hypostomes are strongly associated to cephalons and pygidia and/or are multiple in the same specimen. Thus, they were not included because they may overestimate the number of unique individuals. Because some samples are made up of only a few specimens, both cephalons and pygidia were considered, even if they may represent the same individual. The low abundance suggests that it might be appropriate to assume a near linear relation between number of sclerites and number of specimens (Gilinsky and Bennington 1994).

In our new database, each sample represents a formation or a member. Such precision allows the delimitation of 67

Table 1. Main characteristics of the lithostratigraphic units studied in the biodiversity analysis. FWFB, Fair Weather Wave Base; SWB, Storm Wave Base.

| Stage | Area | Formation | Member | Symbol | Facies | Biotic Reef | Bathymetry | Reference |
|-----------|-----------------|-----------------|------------------|--------|-----------------|-------------|-----------------------|------------------------------|
| Frasnian | Boulonnais | Ferques | | F10 | limestone | no | upon FWFB | Brice 1988 |
| | | Beaulieu | Pâtur | F9 | calcareous marl | no | below FWFB | |
| | | | Noces | F8 | limestone | bioherm | below FWFB | |
| | Namur syncline | Bovesse | | F7 | limestone | biostrome | below FWFB | Da Silva and Boulvain 2012 |
| | Dinant syncline | Neuville | Petit-Mont | F6 | limestone | mud mound | below FWFB | |
| | | | lateral facies | F5 | shaly limestone | no | below FWFB | |
| | | Grand Breux | Boussu-en-Fagnes | | shale | no | below FWFB | |
| | | | Lion | F4 | limestone | mud mound | below FWFB | |
| | | | Bieumont | F3 | limestone | no | below FWFB | |
| | | Moulin Liénaux | Ermitage | F2 | shale | no | below FWFB | |
| | | | Arche | F1 | limestone | mud mound | below FWFB | |
| Givetian | Boulonnais | Blacourt | Couderousse | G6 | limestone | bioherm | upon FWFB | Hubert 2008 |
| | | | Griset | G5 | limestone | bioherm | close FWFB | |
| | Dinant syncline | Fromelennes | | G4 | limestone | bioherm | close FWFB | Boulvain et al. 2009 |
| | | Terres d'Haurs | | G3 | limestone-marl | no | close FWFB | Mabille and Boulvain 2008 |
| | | Trois-Fontaines | | G2 | limestone | bioherm | around FWFB and below | |
| | | Hanonet | | G1 | limestone | bioherm | close FWFB | Mabille and Boulvain 2007b |
| | | X | | E4 | limestone | bioherm | upon FWFB | Préat et al. 2007 |
| Eifeilian | Dinant syncline | Jemelle | | E3 | marl | no | around FWFB and SWB | Mabille and Boulvain 2007a |
| | | Couvin | | E2 | limestone | bioherm | around FWFB and SWB | |
| | | Eau Noire | | E1 | calcareous marl | no | around FWFB and SWB | Crônier and van Viersen 2007 |
| | | | | | | | | |

different assemblages joined with a detailed description of their environment occurring in the same lithological unit.

Although significant progress has been made in the taxonomic description and inventory of Ardenne biodiversity in the last decade, generic identifications are more reliable than specific ones. Although treatment at a generic level can also be difficult (Cecca 2002), multivariate analyses were performed at this level.

Because the diagnoses of two Scutelluinae genera, *Scutellum* and *Goldius*, are still controversial (e.g., Basse 1996; Feist and Talent 2000; Jell and Adrain 2002; Basse and Müller 2004), we chose to consider only the subfamily level. The distinction of these genera is based on the median pygidial segment and the pygidial shape, however, numerous intermediate morphologies of these characters complicate greatly their distinction. Moreover, a generic determination is uncertain because most of specimens are disarticulated. To summarize, 29 taxa (genus or subfamily level) and 67 samples have been considered in our analyses.

Methods

The trilobite database was a subject of statistical analyses in order to understand the distribution patterns of Middle

and Upper Devonian trilobites from the Ardenne Massif and Boulonnais and to identify the relationships between the assemblages and their environment.

Firstly, we performed a Hierarchical Cluster Analysis (HCA) to define discrete assemblages from similar taxonomic composition. It is a clustering method that groups together the recurring samples by levels of taxonomic similarity. The HCA produces a dendrogram showing the relationships within the assemblages (Q mode taking account samples of similar taxonomic composition) and the variable (R mode taking account emphasizing co-occurrence of taxa). HCA was achieved using the average linkage method and similarity was measured with the Pearson correlation index (Hammer and Harper 2006).

Additionally, an analysis of similarities (ANOSIM) has been performed to examine statistically significant differences between groups of taxa (associations). This is a non-parametric test, based upon Bray-Curtis dissimilarity values (Clarke 1993; Hammer and Harper 2006). ANOSIM relies on a test statistic, R, which compares the differences within each group and between the groups. If the associations are significantly different, intra-group similarity is higher than those between groups and the R-value will be closed to 1. Conversely, an R-value close to 0 means that the difference between groups is low and the associations are similar. The

significance of the results is tested with a permutation test (5000 replicates).

To complete the HCA and to identify indirect environmental gradients, we performed a Detrended Correspondence Analysis (DCA). This factor analysis is recommended for palaeoecological studies (Holland et al. 2001; Bonelli and Patzkowsky 2008) as it efficiently reduces the horseshoe effect, formed when samples from first axis extremes have only a little overlap in taxonomic composition. DCA maximises the correspondence between taxa and samples and provides ordination scores for both taxa and samples according to the relative abundance of taxa. DCA reduces the data distortion of a traditional correspondence analysis by dividing the arch into a series of segments and subtracting the mean second axis value for each segment from each score within that segment. For removing unwanted compression near the extremities of the first axis, its scores are rescaled such that there is a constant turnover rate along this axis.

In order to complete the palaeoecological information, we used the Shannon index H' of diversity (Shannon and Weaver 1949), based on abundance matrices.

Where S is the number of samples, p_i is the taxa i proportion compared to the sum of abundances of all species at a particular sample, n_i is the individual number of the taxon i per sample and N is the total number of individuals per sample.

HCA, ANOSIM, DCA, and diversity index were performed using the data-analysis software PAST 2.15 (Hammer et al. 2001).

Results

The hierarchical cluster analysis performed on the relative abundance of 29 taxa for 67 samples (Fig. 3) allows the delimitation of four associations within the Middle and Upper Devonian trilobites of the Ardenne (Belgium and north of France). Three of them were previously defined by Crônier and van Viersen (2007) but a fourth from the Frasnian is new. The Q mode clustering was not able to clearly determine the relationships of some samples. Indeed, cluster analyses have the tendency to break gradients into discrete assemblages; the *Scutellum–Goldius* group attracts some samples (Cou-E2, Nis-E2, Cou-E3, Cou-G1, Rest-G1, and Roch-G1) that probably belong to other associations (see discussion about *Scutellum–Goldius* association for the explanation). However, the sample sorting performed by the DCA (Fig. 4) resolves this issue better than the hierarchical cluster analysis. DCA sample sorting manages transitional distribution and forms more coherent gatherings of these samples.

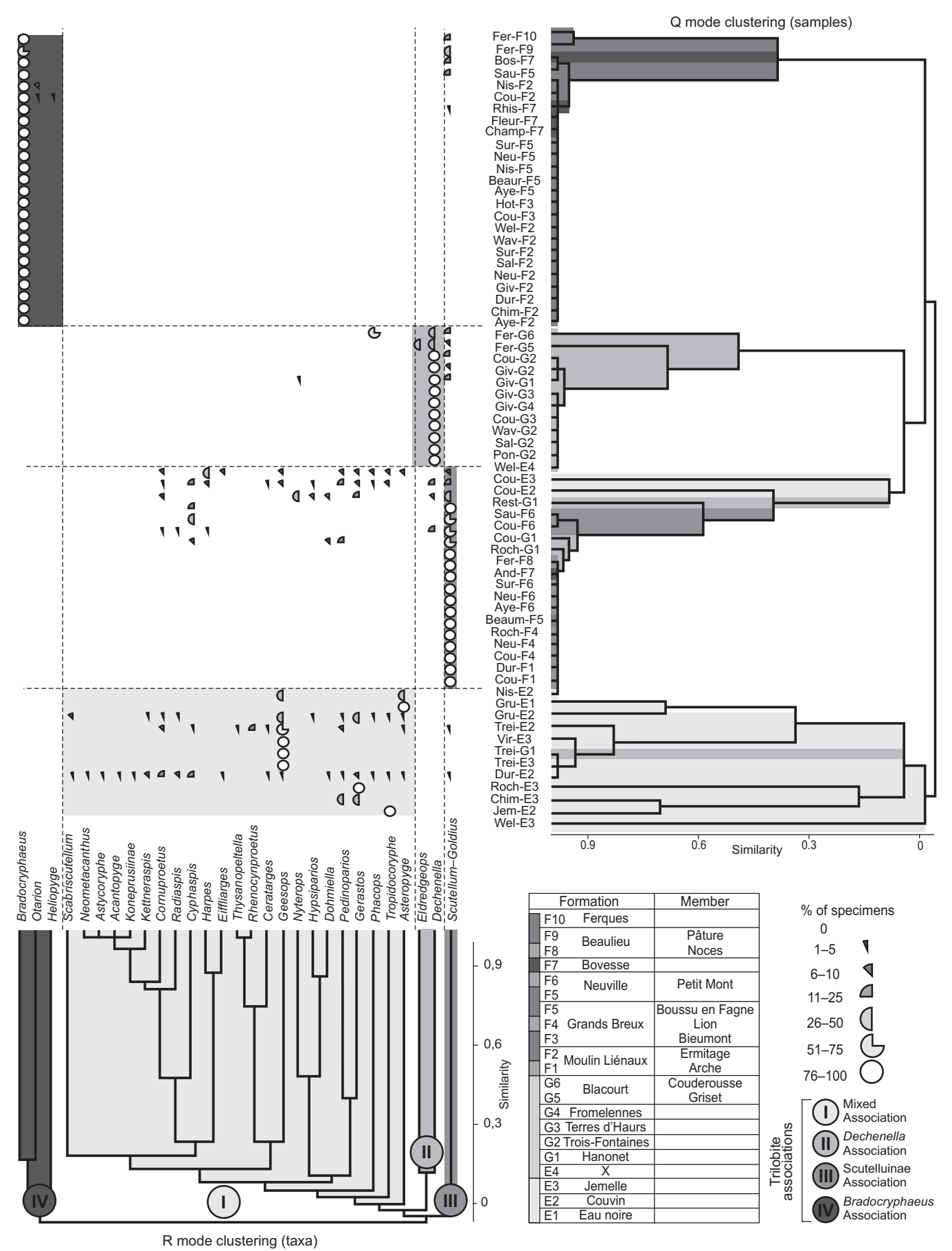
ANOSIM was applied to test for significant differences between the four identified clusters using 5000 permutations and a distance measure (Bray-Curtis index). The R coefficient is 0.847 and the p values is $<0.001^{***}$, providing a significant difference between taxa groupings and supporting the results of the hierarchical cluster analysis.

Trilobite associations (see Fig. 3).—Mixed association: With 22 taxa inventoried, this association presents by far the highest biodiversity values of the massif during the Devonian (Fig. 5). Nevertheless, several samples (Dur-E2, Trei-E3, Trei-G1, Gru-E1, Gru-E2, Jem-E2, Chim-E3, Wel-E3) are represented only by one or two genera. This fauna is characteristic of the Eifelian environments (Eau Noire, Jemelle, and Couvin formations) and is present in most samples from the Hanonet Formation (Lower Givetian). No clear relationship between biodiversity values and the formations was recognised. Although Crônier and van Viersen (2007) distinguished 3 sub-associations, this denomination was not maintained because these groups have only partially been found again in the present analysis and there is no particular relationship with lithostratigraphic units.

Dechenella association: Named *Dechenella* and *Nyterops* association by Crônier and van Viersen (2007). Occurring in only one sample (Giv-G1), the genus *Nyterops* does not appear here to be characteristic of this fauna. The biodiversity is very low compared to the previous association (Fig. 5). Indeed, in most samples only the genus *Dechenella* is represented; though sometimes this genus is accompanied by phacopids (*Phacops*, *Nyterops*, or *Eldredgeops*) and/or Scutelluinae (Fig. 3). The first occurrence of this association is in the X Formation (Upper Eifelian) and continues into the Hanonet Formation (Lower Givetian). This fauna dominates the other Givetian formations (Trois-Fontaines, Terres d’Hairs, Fromelennes).

Scutellum–Goldius association: The HCA (Fig. 3) suggests that the samples Nis-E2, Cou-E2, Cou-E3, Cou-G1, Rest-G1, and Roch-G1 belong to the *Scutellum–Goldius* association. As stated previously, we chose to not strictly follow the hierarchical cluster analysis, because difficulties distinguishing *Scutellum* from *Goldius* disturbs the distribution pattern. Indeed, except for Nis-E2, the biodiversity of these samples is too high (Fig. 5) to be grouped in this association and is in better concordance with the Mixed association. These choices are supported by the DCA results (Fig. 4), grouping Cou-E2 and Cou-E3 with the others Eifelian samples and placing Cou-G1, Rest-G1, and Roch-G1 as transitional forms between the *Scutellum–Goldius* and *Dechenella* associations. In addition, we chose to remove Nis-E2 (Eifelian sample), from the *Scutellum–Goldius* association, because all the other samples occur in the Frasnian (Arche, Lion, and Petit Mont members). The genus *Cyphaspis* has been reported in few samples (Couvin) of this association.

Bradocryphaeus association: Already identified by Crônier and van Viersen (2007) the biodiversity is low as the *Dechenella* and the *Scutellum–Goldius* associations (Fig. 5). Strongly dominated by *Bradocryphaeus*, this genus may be joined by Scutelluinae representatives. The genera *Helioptyge* and *Otarion* are recorded in only one or two samples. This association is restricted to the Frasnian in the reef lateral facies (Ermitage, Bieumont, and Boussu-en-Fagne members, Neuville Formation).



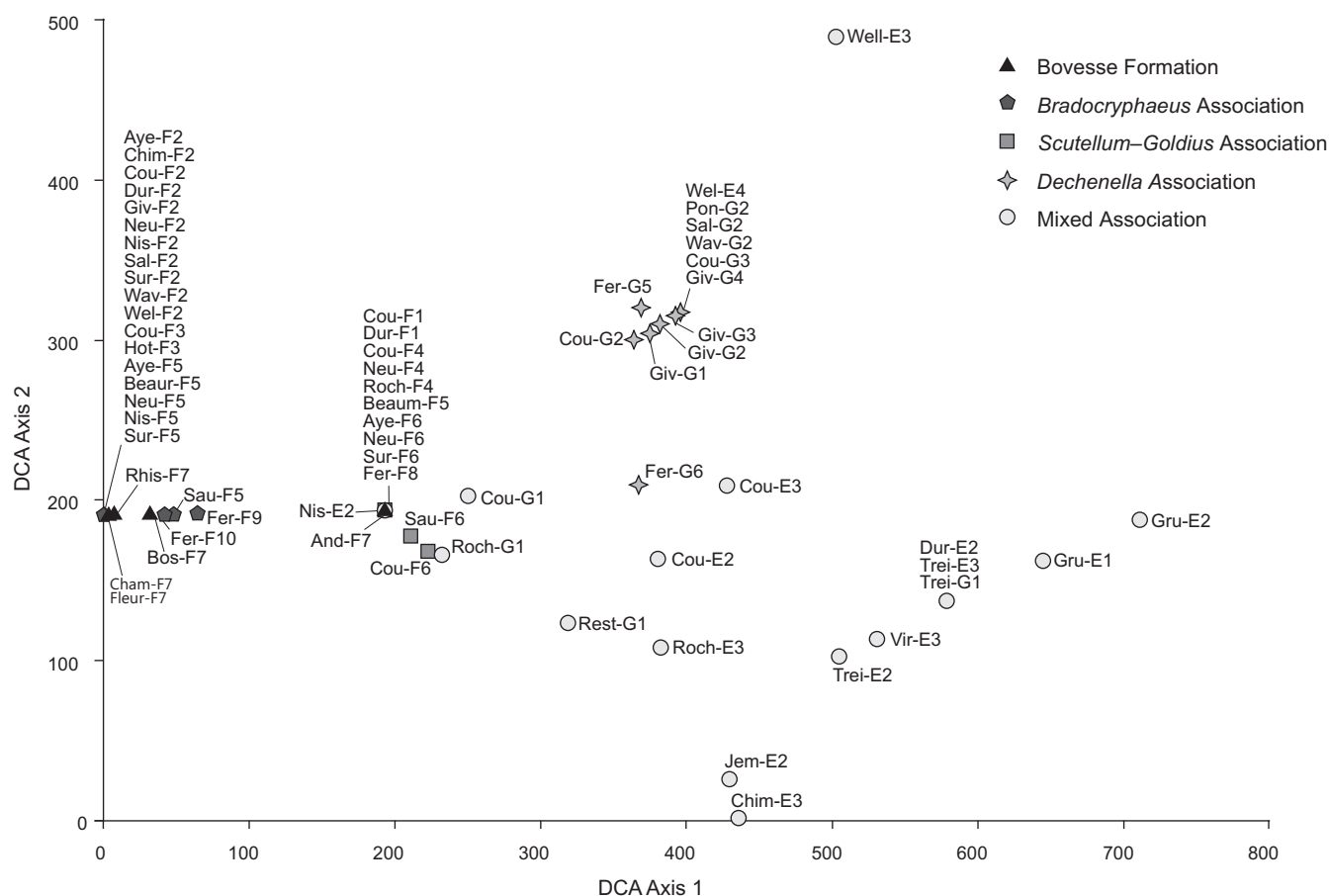


Fig. 4. Scatter plot of 29 trilobite taxa for 67 samples from the Middle and Upper Devonian of the Ardenne Massif and Boulonnais (France, Belgium), according to DCA (see Fig. 2, 3 for abbreviations). The two first axes represent respectively 42.8 and 28.1% of the total variance.

Spatial distribution.—The results of the DCA based on faunal contents are significant (eigenvalues for DC1 and DC2 axes are respectively 0.9683 and 0.6354). The majority of the information is explained by DC1 axis, which clearly reveals a main faunal gradient (Fig. 4).

The occurrence of samples from the Mixed association (high DC1 axis) to the *Bradocryphaeus* association (low DC1 axis) shows the tendency of fauna to co-occur and their alignment may reflect differentiation according to a temporal factor from the oldest (Mixed association) to the youngest (*Bradocryphaeus* and *Scutellum–Goldius* associations). The DCA does not reveal an environmental gradient. Indeed, no ecological factor, such as the bathymetry or reef/ramp facies can be clearly associated with the faunal gradient. However, this analysis suggests that the *Dechenella* association (Givetian) is more closely related to the *Scutellum–Goldius* association (Frasnian) than the *Bradocryphaeus* association (Frasnian). This may be explained

by the fact that the two first associations are more related to the reef environments.

Dinant synclinorium: The distribution of the trilobite associations over the southern border of the Dinant synclinorium is rather homogeneous without any geographic tendency recognisable. HCA and DCA results support this observation because the samples geographically close are not particularly associated in these analyses (Figs. 3, 4).

Namur synclinorium: The samples F7 from the Bovesse Formation are well integrated into the Frasnian *Bradocryphaeus* association identified from the southern part of the Dinant synclinorium. Nevertheless, the easternmost sample (And-F7) is included into the *Scutellum–Goldius* association (Figs. 3, 4) and is represented only by members of this subfamily. The other four samples (Bos-F7, Rhis-F7, Fleur-F7, and Champ-F7) are dominated by the genus *Bradocryphaeus* but some representatives of the Scutelluinae occur in these samples as well.

← Fig. 3. Dendrogram with R and Q modes from hierarchical cluster analysis using the Unweighted Pair Group Method with Arithmetic Mean algorithm, applied to the Middle and Upper Devonian trilobites of the Ardenne Massif and Boulonnais (North of France, Belgium), 29 taxa are clustered according to 67 analysed samples (formations or members). Four clusters (I to IV) are identified. Abbreviations of sections: And, Andenne; Beaum, Beaumont; Beaur, Beaurain; Bos, Bossière; Cham, Champion; Chim, Chimay; Cou, Couvin; Dur, Durbuy; Fer, Ferques; Fleur, Fleurus; Giv, Givet; Gru, Grupont; Hot, Hotton; Jem, Jemelle; Neu, Neuville; Nis, Nismes; Pon, Pondrôme; Rest, Rosteigne; Rhis, Rhisnes; Roch, Rochefort; Sau, Sautour; Sel, Seloigne; Sur, Surice; Trei, Treignes; Vir, Vireux-Molhain; Wav, Wavreille; Wel, Wellin. See Fig. 2 for abbreviations of the formations.

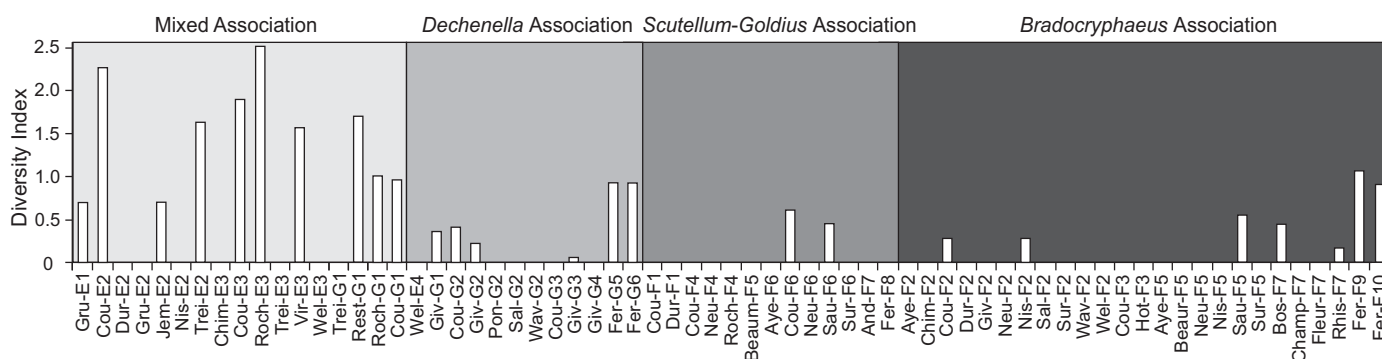


Fig. 5. Diversity (Shannon-Weaver index) of the 67 trilobite samples from the Middle and Upper Devonian of the Ardenne Massif and Boulonnais (North France, Belgium) for four delineated associations (see Figs. 2, 3 for abbreviations).

Boulonnais: The two Givetian samples (G5, Griset and G6, Couderousse members from the Blacourt Formation) of Ferques Massif are integrated into the *Dechenella* association identified in the Ardenne Massif during the same period (Figs. 3, 4). However, the hierarchical cluster analysis highlights a slightly higher biodiversity in this area with the presence of phacopids such as *Phacops* or *Eldredgeops* (Fig. 5).

The sample Fer-F8 from the Noces Member of the Beau-lieu Formation (Frasnian) is tightly integrated to the *Scutellum-Goldius* association (Figs. 3, 4). Indeed, members of this subfamily only represent this sample as it is with those of the Ardenne.

The samples Fer-F9 from the Pâturage Member of the Beau-lieu Formation and Fer-F10 from the Ferques Formation (Frasnian) belong to the *Bradocryphaeus* association. Nevertheless, as with the Givetian, these samples from Boulonnais show higher values of the biodiversity (Fig. 5). Indeed, the record of Scutelluinae specimens in these samples is singular within the *Bradocryphaeus* association. Due to this particularity, HCA and DCA locate these samples in a “marginal” position within this association (Figs. 3, 4).

Discussion

Taphonomy.—Middle and Upper Devonian deposits throughout the Ardenne Massif and the Boulonnais are mostly composed of disarticulated trilobites. These remains are usually interpreted as having undergone a period of exposure before burial (Speyer 1991). Moreover a large number of disarticulated sclerites as compared to partially articulated or complete specimens is indicative of some degree of reworking (Pater-son et al. 2007). Nevertheless, trilobite sclerites are usually complete and do not bear signs of abrasion. Such preservation implies an exposure in a relatively quiet environment where agitation is not able to transport trilobites (Speyer 1991). The fact that the material shows no obvious sign of hydrodynamic sorting supports this assumption.

Tectonics (Variscan orogeny; Mansy and Lacquement 2006) and diagenesis played a significant role on the trilobite preservation in this area. Indeed, specimens are com-

monly found distorted and/or conserved as external/internal moulds (van Viersen 2007a). This reduces both the trilobite abundance and biodiversity between the different studied sections.

It is appropriate to mention the exceptionally well-pre-served deposit called the “Mur des douaniers” in Vireux-Mol-hain (Vir-E3). This Early Eifelian section of the Ardenne Massif is remarkable for its abundance of trilobite remains, numerous articulated sclerites and the species richness (Crôn-ier and van Viersen 2008). The preservation conditions likely represent a significant factor in the high biodiversity (and consequently the high value of the Shannon index; Fig. 5) for this section. Nevertheless, it cannot explain all the richness since others Eifelian deposits, such as Couvin or Rochefort (Cou-E2, Cou-E3, and Roch-E3) have a higher diversity in-dex value but taphonomic conditions that are less suitable for high quality preservation than those of the Vireux-Molhain.

In this way, taphonomic study suggests a reduced trans-port, with fauna contamination between the different forma-tions (or members) for both spatially and temporally being unlikely. However, diagenesis and tectonic conditions have reduced the biodiversity of a significant portion of the sec-tions analysed. Thus, even if the presence of a taxon provides reliable information, absence and abundance data must be interpreted carefully.

Palaeoenvironments of the trilobite associations.—The presence of a reefal system on the Eifelian ramp has no “im-pact” on the trilobite benthic association. Indeed, the Mixed association flourishes on the median ramp (Eau Noire and Jemelle formations; Bultynck and Dejonghe 2001; Dumou-lin and Blockmans 2008; Fig. 6A) and on a barrier locally developed (Couvin Formation; Mabilie and Boulvain 2007a; Fig. 6B). The trilobites are constrained to forereef environ-ments at a similar depth as the median ramp facies. No cor-relation has been recognized between these environments and diversity values or taxonomic composition. Indeed, in both environments the Mixed association may be represented by only one/two genera or more than ten. Unfortunately, we were not able to determine the lithostratigraphic member for most Eifelian samples. Nevertheless, this information exists for Vireux-Molhain (Crônier and van Viersen 2008)

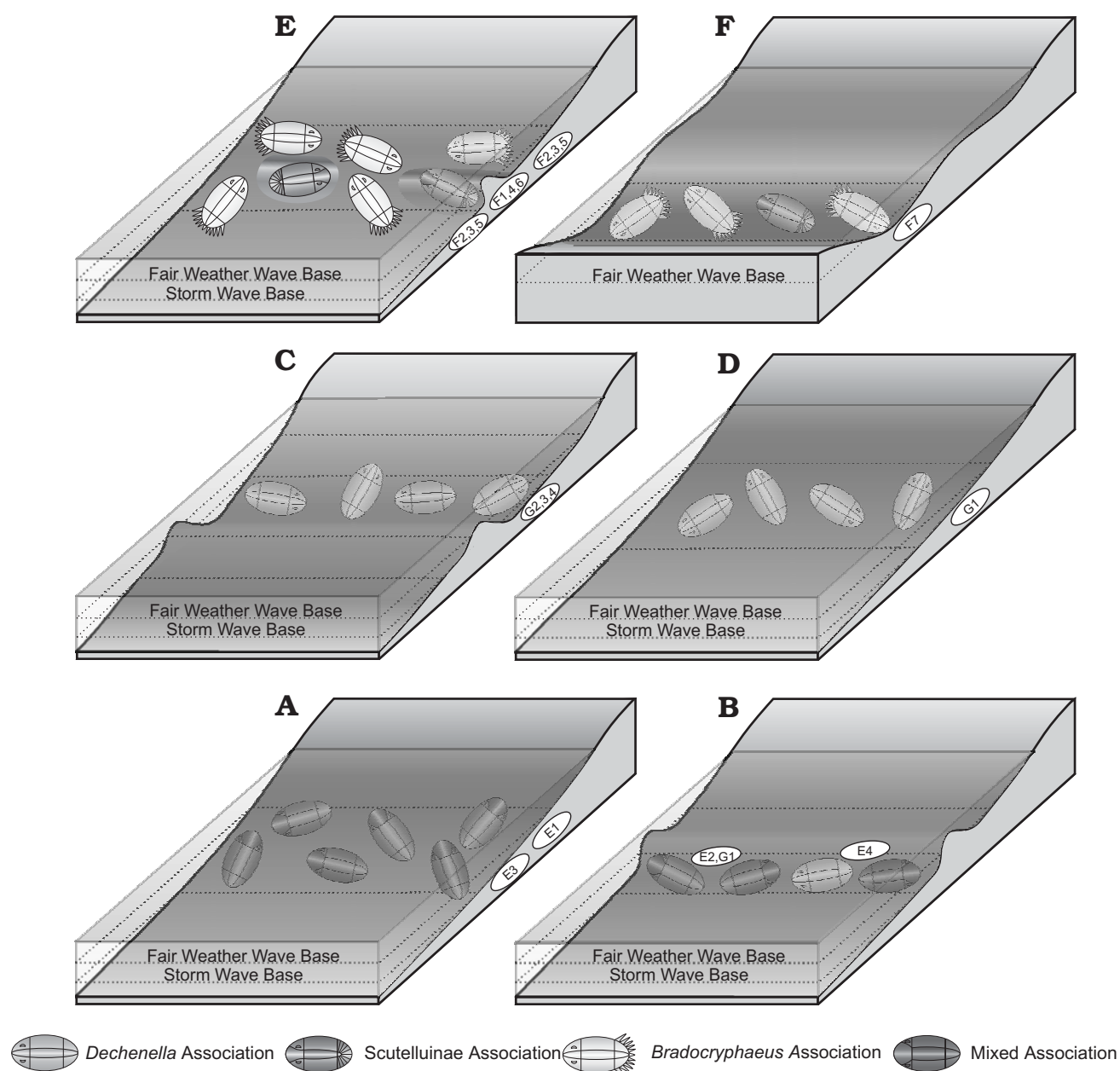


Fig. 6. Distribution of trilobite associations in the southern border of Dinant synclinorium, Ardenne Massif (Belgium, France) during the Middle and Late Devonian (see Fig. 2 for abbreviations). **A.** Eifelian ramp. **B.** Eifelian reef. **C.** Givetian carbonated platform. **D.** Givetian ramp. **E.** Frasnian platform. **F.** Frasnian deep facies of Namur synclinorium.

and Jemelle (van Viersen 2007b). The Mixed association does not appear to be restricted to a specific member of the Jemelle Formation. Along these lines, the respective in Vieux Moulins (silt-clay) and Chavées members (alternating beds of shale and limestone) (sensu Lacquement et al. 2003) samples confirm the environmental tolerance of this fauna.

The *Dechenella* association developed locally (forereef environment of the X Formation Fig. 6B) in Eifelian bioherms and prospered with the development of the Givetian carbonated platform (Mabille et al. 2008; Boulvain et al. 2009; Fig. 6C) encountered in Trois-Fontaines, Terres d'Hairs, and Fromelennes formations (Bignon and Crônier 2011). Contrary to those of the X Formation, trilobites were found in the

backreef between the Fair Weather Wave Base, FWFB and the Storm Wave Base, SWB. In the Upper Givetian carbonated platform of the Boulonnais, the trilobites from this association lived in the same environment, i.e., the back-reef below the FWFB (within Grisot and Couderousse members from the Blacourt Formation; Pelhate and Poncet 1988; Fig. 7A).

For the Frasnian, the trilobite associations are limited to their specific environments and no overlap is recognised (however, Scutelluinae members may occur in some *Bradocryphaeus* association sample). The *Scutellum–Goldius* association is restricted to the mud mound environments (Arche, Lion, and Petit Mont members; Boulvain 2007; Fig. 6E) whereas the *Bradocryphaeus* association occurs only in lat-

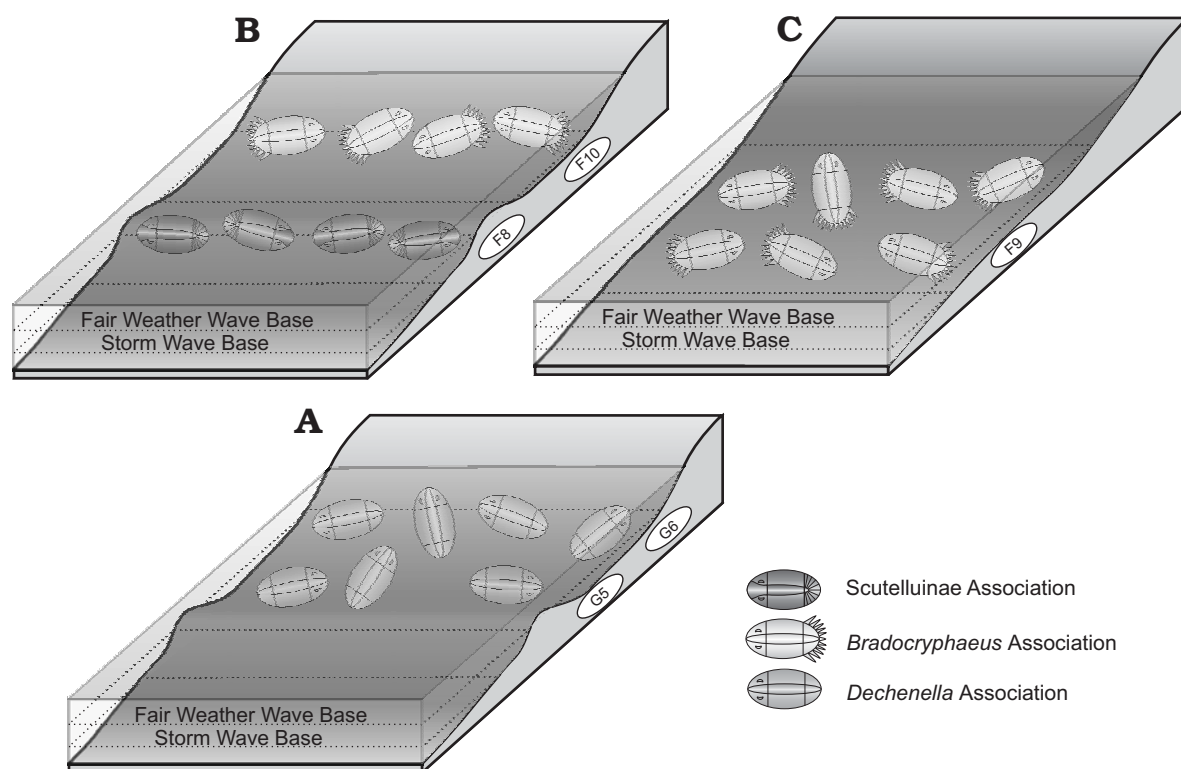


Fig. 7. Distribution of trilobite associations in the Boulonnais (North of France) during the Middle and Upper Devonian (see Fig. 2 for abbreviations). **A.** Givetian carbonated platform. **B.** Frasnian platform. **C.** Frasnian shaly facies.

eral facies of these buildups below the FWWB (Ermitage, Bieumont, and Boussu-en-Fagne members, Neuville Formation; Da Silva and Boulvain 2012; Fig. 6E). In the Namur synclinorium (Bovesse Formation; Fig. 6F), the *Bradocryphaeus* association is the most developed within lateral facies deposited under the FWWC whereas the *Scutellum–Goldius* association is present in biostromes as in Andenne (Da Silva and Boulvain 2012).

The Boulonnais where a barrier was erected several times during the Frasnian is in accordance with the trend observed in the Ardenne Massif. The *Scutellum–Goldius* association flourishes on the reef system (Noce Member, Beaulieu Formation; Brice 1988; Fig. 7B) whereas the representatives of the *Bradocryphaeus* association are restricted in the back reef upon the FWWB or on the median ramp below the FWWB and the SWB (respectively, within the Ferques Formation; Fig. 7B and the Pâturage Member, Beaulieu Formation; Fig. 7C; Brice 1988).

Environmental influence of the benthic faunas.—The composition of trilobite associations seems to be mainly controlled by the rate and type of shelf sedimentation. Indeed, faunal succession has been concomitant with changes in sedimentary regime. The mixed detrital supply and carbonate production of the Eifelian is correlated with the development of the Mixed association. The *Dechenella* association then appears with the carbonate factory initiation during the Early Givetian. Finally this fauna is replaced by the *Bradocryphaeus* and *Scutellum–*

Goldius associations when the platform is drowned and detrital sediments come back.

However, the trilobite communities do not seem to be affected by local or brief modifications of the sedimentary mode. Indeed, the Mixed association, which is characteristic of ramp facies, occurs in a reef system within the Couvin Formation without particular difference in its structure. The same trend exists with the *Dechenella* association, but to a lesser degree. Indeed, this association is mainly encountered in the formations where a reefal complex is developed but still persists within levels where ramp facies are quickly developed (Bignon and Crônier 2011).

Contrary to the Eifelian and Givetian associations, the Frasnian communities are strongly tied to their environment. These faunas constitute valuable facies indicators: the *Scutellum–Goldius* association is linked to carbonate buildups and biostromes, while the *Bradocryphaeus* association is restricted to the lateral facies of these structures. Nevertheless, this latter fauna is not restricted to a detrital sedimentation, and reveals its presence in the carbonate lateral facies from the Neuville (Ardenne Massif) and Ferques (Boulonnais) formations.

Terminal Eifelian global biotic event.—The global biotic Kačák event (House 1985) was a sudden onset of the oxygen-depleted zone lead by a rapid transgression. This event was developed in successive phases during the uppermost part of the Eifelian and finished at the end of *Polygnathus ensensis* Conodont Zone, just before the Eifelian–Givetian

boundary (House 2001). The resulting black-shales facies (Kačák interval) lasted for at least one million years (Schöne 1997). In Ardenne Massif, this event is contemporary to the lower part of the Hanonet Formation (Bultynck and Dejonghe 2001). The samples described in the Hanonet Formation are shared (Fig. 3) between the *Scutellum–Goldius* association (Cou-G1, Rest-G1, and Roch-G1), the Mixed association (Trei-G1), and the *Dechenella* association (Giv-G1). The sample from Givet, showing clear Givetian affinities (Figs. 3, 4), occurs in the upper part of the Hanonet Formation (Bignon and Crônier 2011) and is posterior to the Kačák event. The samples from Couvin, Rochefort, and Treignes come from Mailleux field works (Mailleux 1919), unfortunately the temporal constraint could not be more precise than the formation. Nevertheless, the Treignes sample is well integrated in the Mixed association described in the HCA (Fig. 3) and DCA (Fig. 4). Moreover, the occurrence of *Geesops*, a genus characteristic of the Eifelian faunas (van Viersen 2007b), strengthens the assumption that this sample comes from the lower part of the Hanonet formation before or during the Kačák event (House 1985). The remaining samples (Cou-G1, Rest-G1, and Roch-G1) are included in the *Scutellum–Goldius* association in the HCA. Nevertheless, the DCA (Fig. 4) shows these samples more as a transition between this association and the Mixed association, and this is particularly obvious with the Resteignes sample. Moreover, the diversity indexes for these communities (Fig. 5) are high and similar to the Mixed association values. The trilobites from Resteigne were sampled in the lower part of the Hanonet Formation (van Viersen 2007b) before the Kačák interval end. We may reasonably assume that the samples of Couvin and Rochefort come from similar layers before the substitution of the Eifelian fauna by the Givetian one. As illustrated by Budil (1995) and Schöne (1997) the faunal extinction was progressive and the quick appearance of new taxa has been recorded during this interval. These samples in the Ardenne Massif may be another example of a progressive substitution of fauna during the Kačák interval, with the *Dechenella* association replacing the Mixed association.

Environmental specialisation on Frasnian associations.—The lower Frasnian represents the acme of the transgressive phase that began in the Middle Devonian (Haq and Schutter 2008). The high sea level led to the flooding of the Givetian carbonate platform. Consequently, isolated carbonate mud mounts lie on a siliciclastic ramp (Boulvain et al. 1999). In this context, the Ardenne Asteropyginae flourishes exclusively in lateral facies of the buildups (*Bradocryphaeus* association). The trend of high sea levels homogenised the facies and other Frasnian Asteropyginae occurred in similar environments all over the world. In the Eifel Massif (Germany), the genus *Bradocryphaeus* is present in calcareous shales (Basse and Müller 2004). The representatives of this genus, in the Armorican Massif (France), occur in shale and sandstone facies (Morzadec 1983). Smeenk (1983) described in the Frasnian of Cantabrian Mountains (Spain) several As-

teropyginae, in reef facies and the clastic shelf of the Nocado Formation. Nevertheless, a posterior conodont study (Keller and Grötsch 1990) attributed a Givetian age to the Nocado Formation. Looking far toward the East, several Asteropyginae genera were recorded in northern Gondwana. In Iran, specimens are found in limestone with a significant terrigenous influence, not below the storm wave base (Morzadec 2002) and in a shallow quiet argillite (Ghobadi Pour et al. 2013). In Afghanistan, the Asteropyginae are described in grey limestone sometimes with siliciclastic influences (Farsan 1981).

The Illaenidae, a group close to the Scutelluidae, were able to arch their thorax in a concave-upward position. This flexibility suggests that this group was adapted to uneven surfaces such as those in and around bioherms (Whittington 1997). Indeed, in the Ordovician (Carlucci and Westrop 2012) and Silurian (Hughes and Thomas 2011) this group has shown a clear affinity with these environments. Thus, it is not surprising that the *Scutellum–Goldius* association occurs mainly in the Frasnian buildups of the Ardenne Massif. Some *Scutellum* members are described in the lower Frasnian buildups of the Holy Cross Mountains in Poland (Chlupáč 1993). However, during the Givetian the scutelluids are not so restricted to bioherms. Indeed, they occur in marly limestone of the Holy Cross Mountains (Kielan 1954), in ramp facies of the Ardenne Massif (Bignon and Crônier 2011) or lateral facies of the Eifel (Basse 1996).

The same trend is recognizable between Asteropyginae and the *Scutellum–Goldius* morphotype. During the Givetian, these groups were eurytopic whereas during the Frasnian their ecological tolerances were more restricted to a particular environment.

Concluding remarks

During the Devonian of Ardenne Massif and Boulonnais, reef ecosystems seem to be progressively more disparate from the others environments of the continental shelf. The Eifelian trilobite fauna of the Mixed association flourished either in ramp or platform facies whereas Givetian *Dechenella* association showed a predilection for reef system. This distinctiveness of the reef was more expressed during the Frasnian due to the restriction of the *Bradocryphaeus* and *Scutellum–Goldius* associations to only one type of environment, mud mounts and lateral facies, respectively.

We are aware that a single taxonomic group can not alone exhaustively illustrate the process of progressive differentiation of a reef. The signal identified from a single group may reflect a number of other processes (e.g., migration or in-group competition) occurring in the fauna. Therefore a comparison with the biodiversity of others taxonomic groups is essential to more accurately interpret the changing environment. A comparison with other non-builder benthic organisms such brachiopods and ostracods occurring in the same rock formation may provide the necessary information.

Several studies on these group occurring in the Devonian of the Ardenne Massif have been published recently (e.g., brachiopods, Godefroid and Mottequin 2005; Brice et al. 2008; Mottequin 2008; ostracods, Casier and Pr  at 2006; Casier and Olempska 2008; Casier et al. 2013) and they may provide an implement to our study of biodiversity. In the near future, these data will be analysed together in a forthcoming study to provide a more complex evaluation of the long-term fluctuations in the Devonian environment.

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References

- Asselbergs, E. 1912. Description d'une faune frasnienne inf  rieure du bord nord du Bassin de Namur. *Bulletin de la Soci  t   belge de G  ologie, de Pal  ontologie et d'Hydrologie* 36 (1): 1–47.
- Asselbergs, E. 1946. L'  od  vonian de l'Ardenne et des R  gions voisines. *M  moires de l'Institut G  ologique de l'Universit   de Louvain* 14: 1–598.
- Averbuch, O., Tribouvillard, N., Devleeschouwer, X., Riquier, L., Mistiaen, B., and van Vliet-Lanoe, B. 2005. Mountain building-enhanced continental weathering and organic carbon burial as major causes for climatic cooling at the Frasnian–Famennian boundary (c. 376 Ma)? *Terra Nova* 17: 1–93.
- Basse, M. 1996. Trilobiten aus mittlerem Devon des Rhenohercynikums: I. Corynexochida und Proetida (1). *Palaeontographica Abteilung A* 239: 89–182.
- Basse, M. and M  ller, P. 2004. *Eifel-Trilobiten III. Corynexochida, Proetida (2), Harpetida, Phacopida (2), Lichida*. 260 pp. Quelle and Meyer Verlag, Wiebelsheim.
- Bignon, A. and Cr  nier, C. 2011. Middle Devonian trilobites from the Mont d'Hairs section in Givet, France, with two new species of *Dichenella*. *Transactions of The Royal Society of Edinburgh* 102: 43–57.
- Bonelli, J.R. and Patzkowsky, M.E. 2008. How are global patterns of faunal turnover expressed at regional scales? Evidence from Upper Mississippian (Chesterian Series), Illinois Basin, USA. *Palaaios* 23 (11): 760–772.
- Boulvain, F. 2001. Facies architecture and diagenesis of Belgian Late Frasnian carbonate mounds. *Sedimentary Geology* 145: 269–294.
- Boulvain, F. 2007. Frasnian carbonate mounds from Belgium: sedimentology and palaeoceanography. In: J.J. Alvaro, M. Aretz, F. Boulvain, A. Munnecke, D. Vachard, and E. Vennin (eds.), *Palaeozoic Reefs and Bioaccumulations: Climatic and Evolutionary Controls. Geological Society of London, Special Publication* 275: 255–274.
- Boulvain, F., Bultynck, P., Coen, M., Coen-Aubert, M., Helsen, S., Lacroix, D., Laloux, M., Casier, J.G., Dejonghe, L., Dumoulin, V., Ghysel, P., Godefroid, J., Mouravieff, N., Sartenaer, P., Tourneur, F., and Vanguestaine, M. 1999. Les formations du Frasnien de la Belgique. *Memoirs of the Geological Survey of Belgium* 44: 1–125.
- Boulvain, F., Mabilille, C., Poulain, G., and Da Silva, A.-C. 2009. Towards a palaeogeographical and sequential framework for the Givetian of Belgium. *Geologica Belgica* 12: 161–178.
- Brice, D. 1988. Le D  vonian de Ferques (Boulonnais–France) historique. Synth  se des donn  es nouvelles en stratigraphie, s  dimentologie, pal  ontologie et tectonique. Conclusions. In: D. Brice (ed.), *Le D  vonian de Ferques. Bas-Boulonnais (N. France). Biostratigraphie du Pal  ozo  que* 7: 7–24.
- Brice, D., Bultynck, P., Colbeaux J.P., Lethiers, F., Mistiaen, B., Rohart, J.C., and Bigey, F. 1979. Une nouvelle coupe dans le D  vonian de Ferques (Boulonnais, France). *Annales de la Soci  t   g  ologique du Nord* 96: 135–155.
- Brice, D., Mottequin, B., and Loones, C. 2008. Discovery of new Givetian (Devonian) brachiopods from Boulonnais (N France). *Annales de la Soci  t   g  ologique du Nord* 15 (2): 1–13.
- Budil, P. 1995. Demonstrations of the Ka    k event (Middle Devonian, uppermost Eifelian) at some Barrandian localities. *V  stnik   esk  ho geologick  ho   stavu* 70 (4): 1–24.
- Bultynck, P. and Dejonghe, L. 2001. Devonian lithostratigraphic units (Belgium). *Geologica Belgica* 4: 39–69.
- Carlucci, J.R. and Westrop, S.R. 2012. Trilobite biofacies along an Ordovician (Sandbian) carbonate buildup to Basin Gradient, southwestern Virginia. *Palaaios* 27: 19–34.
- Casier, J.-G. and Olempska, E. 2008. Early Frasnian ostracods from the Arche quarry (Dinant Synclinorium, Belgium) and the *Palmatolepis punctata* Isotopic Event. *Acta Palaeontologica Polonica* 53: 635–646.
- Casier, J.-G. and Pr  at, A. 2006. Ostracods and lithofacies close to the Eifelian–Givetian boundary (Devonian) at Aisemont (Namur Synclinorium, Belgium). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre* 76: 5–29.
- Casier, J.-G., Devleeschouwer, X., Maill  t, S., Petitclerc, E., and Pr  at, A. 2013. Ostracods and rock facies across the Givetian/Frasnian boundary interval in the Sourd D'ave section at Ave-et-Auffe (Dinant Synclinorium, Ardenne, Belgium). *Bulletin of Geosciences* 88: 241–264.
- Cecca, F. 2002. *Palaeobiogeography of Marine Fossil Invertebrates. Concepts and Methods*. 273 pp. Taylor & Francis, London.
- Chlup    , I. 1993. Trilobites from the Givetian and Frasnian of the Holy Cross Mountains. *Acta Palaeontologica Polonica* 37: 395–406.
- Clarke, K.R. 1993. Non-parametric multivariate analysis of changes in community structure. *Australian Journal of Ecology* 18: 117–143.
- Cr  nier, C. and van Viersen, A.P. 2007. Trilobite palaeobiodiversity during the Devonian in the Ardennes Massif. *Bulletin de la Soci  t   G  ologique de France* 178: 473–483.
- Cr  nier, C. and van Viersen, A.P. 2008. The 'Mur des douaniers' an exceptionally well-preserved Early Eifelian fossil site. *Bulletin de la Soci  t   G  ologique de France* 179: 89–95.
- Da Silva, A.-C. and Boulvain, F. 2012. Analysis of the Devonian (Frasnian) platform from Belgium: a multi-faceted approach for basin evolution reconstruction. *Basin Research* 24: 338–356.
- Dumoulin, V. and Blockmans, S. 2008. Le passage l  t  ral entre les formations de Couvin et de Jemelle (Eif  lien) au bord sud du Synclinorium de Dinant (Belgique): introduction du membre du Vieux Moulin–Formation de Jemelle. *Geologica Belgica* 11: 25–33.
- Farsan, N.M. 1981. New Asteropyginae (Trilobita) from the Devonian of Afghanistan. *Palaeontographica Abteilung A* 176: 158–171.
- Feist, R. and Talent, J.A. 2000. Devonian trilobites from the Broken River region of northeastern Australia. *Records of the Australian Museum, Supplement* 58: 65–80.
- Ghobadi Pour, M., Popov, L.E., Hosseini, M., Adhamian, A., and Yazdi, M. 2013. Late Devonian (Frasnian) trilobites and brachiopods from the Soh area, Central Iran. *Memoirs of the Association of Australasian Palaeontologists* 44: 149–158.
- Gilinsky, N.L. and Bennington, J.B. 1994. Estimating numbers of whole individuals from collections of body parts: A taphonomic limitation of the paleontological record. *Paleobiology* 20: 245–258.

- Godefroid, J. and Mottequin, B. 2005. Givetian brachiopods from the Trois-Fontaines Formation at Marenne (Belgium, Dinant Synclinorium). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre* 75: 5–23.
- Hammer, Ø. and Harper, D.A.T. 2006. *Paleontological Data Analysis*. 351 pp. Blackwell Publishing, Oxford.
- Hammer, Ø., Harper, D.A.T., and Ryan, P.D. 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4 (1): 1–9. http://palaeo-electronica.org/2001_1/past/issue1_01.htm.
- Haq, B.U. and Schutter, S.R. 2008. A chronology of Paleozoic sea-level changes. *Science* 322: 64–68.
- Harnik, P.G. 2009. Unveiling rare diversity by integrating museum, literature and field data. *Paleobiology* 35: 190–208.
- Holland, S.M., Miller, A.I., Meyer, D.L., and Dattilo, B.F. 2001. The detection and importance of subtle biofacies within a single lithofacies: The Upper Ordovician Kope Formation of the Cincinnati, Ohio region. *Palaio* 16: 205–217.
- House, M.R. 1985. Correlation of mid-Palaeozoic ammonoid evolutionary events with global sedimentary perturbations. *Nature* 313: 17–22.
- House, M.R. 2002. Strength, timing, setting and cause of mid-Palaeozoic extinctions. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 181: 5–25.
- Hubert, B.L.M. 2008. *Les stromatopores givétiens et frasnien de l'Ardenne méridionale et du Boulonnais (France et Belgique): sédimentologie, paléobiodiversité et paléobiogéographie*. 316 pp. Thèse de doctorat de l'Université Catholique de Lille, de l'Université des Sciences et Technologies de Lille et de l'Université de Liège, Lille and Liège.
- Hubert, B.L.M., Zapalski, M.K., Nicollin, J.-P., Mistiaen, B., and Brice, D. 2007. Selected benthic faunas from the Devonian of the Ardennes: an estimation of palaeobiodiversity. *Acta Geologica Polonica* 57: 223–262.
- Hughes, H.E. and Thomas, A.T. 2011. Trilobite associations, taphonomy, lithofacies and environments of the Silurian reefs of North Greenland. *Palaeogeography, Palaeoclimatology, Palaeoecology* 302: 142–155.
- Jell, P.A. and Adrain, J.M. 2002. Available generic names for trilobites. *Memoirs of the Queensland Museum* 48: 331–553.
- Johnson, J.G., Klapper, G., and Sandberg, C.A. 1985. Devonian eustatic fluctuations in Euramerica. *Geological Society of America, Bulletin* 96: 567–587.
- Kasimi, R. and Prétat, A. 1996. Sédimentation de rampe mixte silico-carbonatée des couches de transition eiféliennes-givéliennes franco-belges. Deuxième partie: Cyclostratigraphie et paléostratigraphie. *Bulletin des Centres Recherches Exploration Production Elf-Aquitaine* 20 (1): 61–90.
- Kielan, Z. 1954. Les trilobites mésodévonien des Monts de Sainte-Croix. *Palaeontologia Polonica* 6: 1–49.
- Keller, M. and Grötsch, J. 1990. Depositional history and conodont biostratigraphy of the Lower Devonian La Vid Group in the Luna area (Cantabrian Mountains, NW Spain). *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* 1990 (3): 141–164.
- Lacquement, F., Mansy, J.-L., Meilliez, F., Van Vliet Lanoé, B., Coen, M., Corneille, J.-P., Dumoulin, V., Hanot, F., Lemonne, E., Oudoire, T., and Penisson, J.-P. 2003. *Notice explicative de la carte géologique de la France (1/50 000)*. Feuille n° 40 Givet 2ème édition. Éditions du BRGM, Orléans.
- Mabille, C. and Boulvain, F. 2007a. Sedimentology and magnetic susceptibility of the Couvin Formation (Eifelian, south western Belgium): carbonate platform initiation in a hostile world. *Geologica Belgica* 10: 47–67.
- Mabille, C. and Boulvain, F. 2007b. Sedimentology and magnetic susceptibility of the Upper Eifelian–Lower Givetian (Middle Devonian) in SW Belgium: insights into carbonate platform initiation. In: J.J. Alvaro, M. Aretz, F. Boulvain, A. Munnecke, D. Vachard, and E. Vennin (eds.), *Palaeozoic Reefs and Bioaccumulations: Climatic and Evolutionary Controls*. *Geological Society of London, Special Publication* 275: 109–123.
- Mabille, C. and Boulvain, F. 2008. Les Monts de Baileux section: detailed sedimentology and magnetic susceptibility of Hanonet, Trois-Fontaines and Terres d'Haus Formations (Eifelian/Givetian boundary and Lower Givetian, SW Belgium). *Geologica Belgica* 11: 93–121.
- Mabille, C., De Wilde, C., Hubert, B., Boulvain, F., and Da Silva, A.-C. 2008. Detailed sedimentology of a non-classical succession for Trois-Fontaines and Terres d'Haus Formations (Lower Givetian, Marenne, Belgium)—Introduction of the Marenne Member. *Geologica Belgica* 11: 217–238.
- Magrean, B. and van Vierssen, A.P. 2005. Revision of Devonian trilobites from Belgium—Part 1. The genera *Cornuproetus* and *Radiaspis*. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 75: 87–93.
- Mailleux, E. 1904. Quelques mots sur les trilobites du Couvinien des environs de Couvin. *Bulletin de la Société belge de Géologie, de Paléontologie et d'Hydrologie* 17: 579–582.
- Mailleux, E. 1909. Etude comparative de la répartition des espèces fossiles dans le Frasnien inférieur du bord méridional du bassin dinantais et dans les niveaux synchroniques du Boulonnais. *Bulletin de la Société belge de Géologie, de Paléontologie et d'Hydrologie* 23: 115–151.
- Mailleux, E. 1919. Remarques sur la faune trilobitique de l'assise des schistes et calcaires à *Calceola sandalina* du bord sud du Bassin de Dinant. *Bulletin de la Société belge de Géologie, de Paléontologie et d'Hydrologie* 29: 52–55.
- Mailleux, E. 1927. Sur les trilobites du Frasnien de la Belgique. *Bulletin de la Société belge de Géologie, de Paléontologie et d'Hydrologie* 37: 77–87.
- Mailleux, E. 1933. *Terrains, roches et fossiles de la Belgique*. 217 pp. Musée royal d'Histoire naturelle de Belgique, Bruxelles.
- Mailleux, E. 1938. Le Couvinien de l'Ardenne et ses faunes. *Mémoires du Musée royal d'Histoire Naturelle de Belgique* 83: 3–57.
- Mansy, J.L. and Lacquement, F. 2006. Contexte géologique régional: l'Ardenne paléozoïque (Nord de la France et Sud de la Belgique). *Géologie de la France* 1–2: 7–13.
- McKerrow, W. and Scotese, C.R. 1990. Palaeozoic Palaeogeography and Biogeography. *Geological Society of London, Memoir* 12: 1–435 pp.
- Morzadec, P. 1983. Le Dévonien (Emsien–Faménien) de la rade de Brest (Massif Armoricain). *Palaeontographica Abteilung A* 181: 103–184.
- Morzadec, P. 1988. Trilobites du Givétien et du Frasnien de Ferques (Boulonnais-France). In: D. Brice (ed.), *Le Dévonien de Ferques*. Bas-Boulonnais (N. France). *Biostratigraphie du Paléozoïque* 7: 493–502.
- Morzadec, P. 2002. Trilobites *Asteropyginae* dévoniens d'Iran. *Geobios* 35: 411–427.
- Morzadec, P., Brice, D., and Loones, C. 2007. Trilobites dévoniens de Ferques, Boulonnais, Nord de la France: Migrations et Paléobiogéographie. *Annales de la Société géologique du Nord* 14 (2): 23–28.
- Mottequin, B. 2008. New observations on Upper brachiopods from the Namur-Dinant Basin (Belgium). *Geodiversitas* 30: 455–537.
- Paterson, J.R., Jago, J.B., Brock, G.A., and Gehling, J.G. 2007. Taphonomy and palaeoecology of the emuellid trilobite *Balcorania dailyi* (early Cambrian, South Australia). *Palaeogeography, Palaeoclimatology, Palaeoecology* 249: 302–321.
- Pelhat, A. and Poncet, J. 1988. Evolution sédimentaire de la Formation de Blacourt (Givétien de Ferques-Boulonnais). In: D. Brice (ed.), *Le Dévonien de Ferques*. Bas-Boulonnais (N. France). *Biostratigraphie du Paléozoïque* 7: 25–37.
- Prétat A. and Mamet, B. 1989. Sédimentation de la plate-forme carbonate givélienne franco-belge. *Bulletin des Centres de Recherches Exploration-Production Elf-aquitaines* 13 (1): 47–86.
- Prétat, A., Blockmans, S., Capette, L., Dumoulin, V., and Mamet, B. 2007. Microfacies d'une lentille biohermale à la limite Eifélien/Givétien ("Fonfry des chiens", Nismes, bord sud du synclinorium de Dinant). *Geologica Belgica* 10: 3–25.
- Richter, R. and Richter, E. 1918. Neue Proetus-Arten aus dem Eifler Mitteldevon. *Zentralblatt für Mineralogie, Geologie und Paläontologie* 1918: 64–70.
- Richter, R. and Richter, E. 1926. Die Trilobiten des Oberdevons. *Beiträge*

- zur Kenntnis devonischer Trilobiten. IV. *Abhandlungen der Preußischen Geologischen Landesanstalt, Neue Folge* 99: 1–314.
- Shannon, C.E. and Weaver, W. 1949. *The Mathematical Theory of Communication*. 125 pp. University of Illinois Press, Urbana.
- Schöne, B.R. 1997. Der *otomari*-Event und seine Auswirkungen auf die Fazies des Rhenohercynischen Schelfs (Devon, Rheinisches Schiefergebirge). *Göttinger Arbeiten zur Geologie und Paläontologie* 70: 1–140.
- Smeenk, Z. 1983. Devonian trilobites of the southern Cantabrian Mountains (northern Spain) with a systematic description of the Asteropyginae. *Leidse Geologische Mededelingen* 52: 383–511.
- Speyer, S.E. 1991. Trilobite taphonomy: a basis for comparative studies of arthropod preservation, functional anatomy and behaviour. In: S.K. Donovan (ed.), *The Processes of Fossilization*, 194–219. Belhaven Press, London.
- Thompson, W.L. 2004. *Sampling Rare or Elusive Species*. 429 pp. Island Press, Washington, D.C.
- van Viersen, A.P. 2006. New Middle Devonian trilobites from Vireux-Molhain (Ardennes, northern France). *Senckenbergiana lethaea* 86: 63–75.
- van Viersen, A.P. 2007a. Kettneraspis, Radiaspis and Ceratarges (Trilobite) from the Middle Devonian of the Rochefort area (Ardennes, Belgium). *Scripta Geologica* 134: 1–18.
- van Viersen, A.P. 2007b. Preliminary report of trilobites from the Hanonet Formation (Eifelian–Givetian transition), southern border of Dinant Synclinorium, Belgium. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 77: 15–29.
- van Viersen, A.P. and Bignon, A. 2011. Late Devonian (Frasnian) asteropygine trilobites from the Frasnies area, southern border of Dinant Synclinorium, Belgium. *Geologica Belgica* 14: 109–128.
- van Viersen, A.P. and Prescher, H. 2009. Trilobites from the Longlier Formation (Lower Devonian; Neufchâteau Synclinorium, southeast Belgium): first record of Pragian associated “Rhenish” and “Bohemian” assemblages from the Ardennes. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 79: 5–26.
- van Viersen, A.P. and Prescher, H. 2010. Taxonomy and biostratigraphy of some proetid trilobites in the Middle Devonian of the Ardennes and Eifel (Rhenohercynian Zone). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 80: 5–45.
- Whittington, H.B. 1997. Illaenidae (Trilobita): morphology of thorax, classification, and mode of life. *Journal of Paleontology* 71: 878–896.
- Ziegler, A.P. 1982. *Geological Atlas of Western and Central Europe*. 130 pp. Shell Internationale Petroleum, Maatschappij.