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

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Bignon, A. and Crônier, C. 2015. Trilobite faunal dynamics on the Devonian continental shelves of the Ardenne Massif and Boulonnais (France, Belgium). *Acta Palaeontologica Polonica* 60 (4): 949–962.

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 detritic 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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Received 15 August 2013, accepted 10 March 2014, available online 25 March 2014.

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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.

http://dx.doi.org/10.4202/app.00019.2013

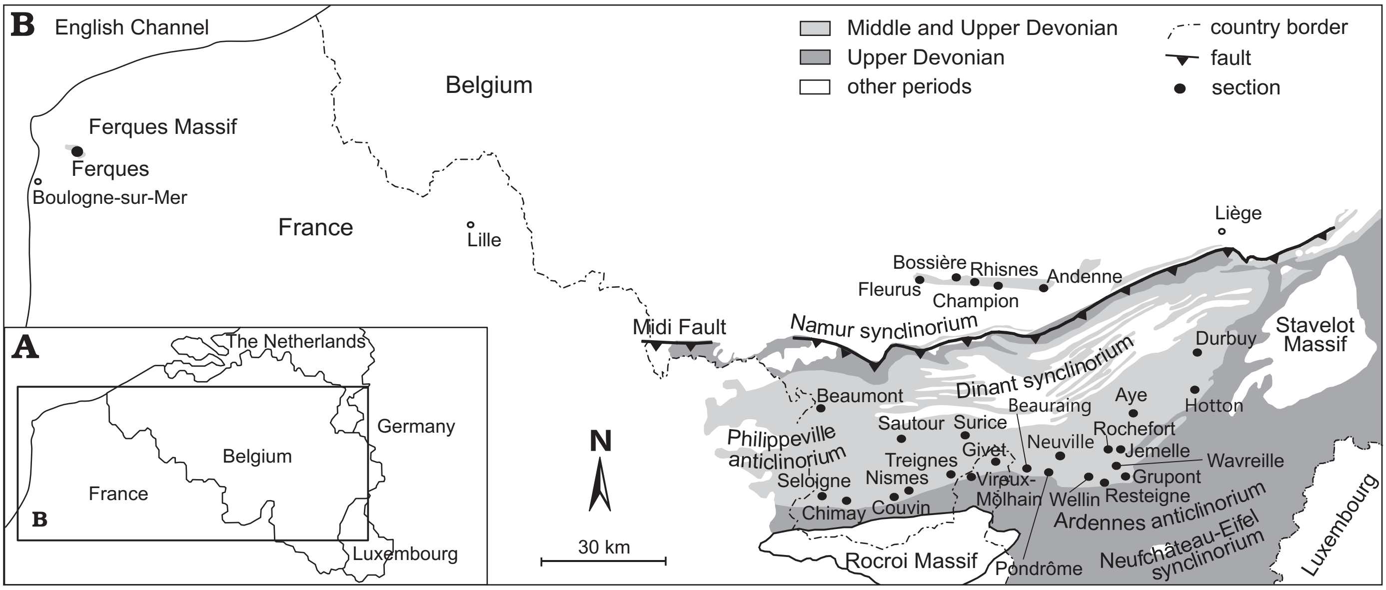


Fig. 1. Geographic location of the studied area (**A**) and geological map of the Ardenne and Boulonnais areas (**B**) with studied fossiliferous sections (modified after Crônier and van Viersen 2007).

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, Ardenne 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 south-eastern 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.

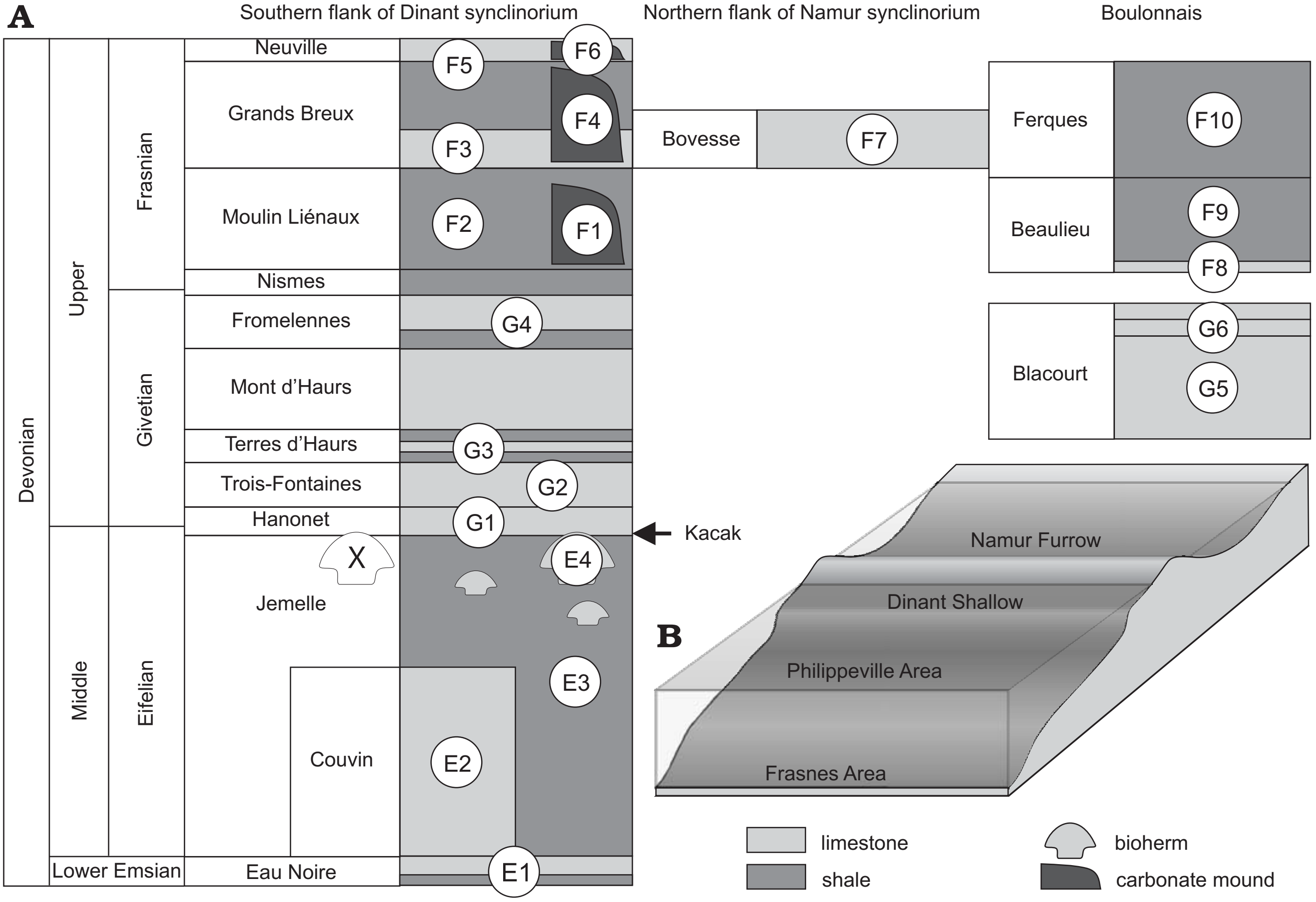


Fig. 2. Generalized lithostatigraphic section of Middle and Upper Devonian of the Ardenne Massif (France-Belgium) and Boulonnais (France) **A**. Correlation of the Ardenne Massif and Boulonnais formations. E1, Eau Noire Formation; E2, Couvin Formation; E3, Jemelle Formation; E4, X Formation; G1, Hanonet Formation; G2, Trois-Fontaines Formation; G3, Terres d'Haurs 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, Pâture 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., Mailleux 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 cephala 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 cephala 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. FWWB, 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 FWWB	Brice 1988
		Beaulieu	Pâture	F9	calcareous marl	no	below FWWB	
			Noces	F8	limestone	bioherm	below FWWB	
	Namur syncline	Bovesse		F7	limestone	biostrome	below FWWB	Da Silva and Boulvain 2012
	Dinant syncline	Neuville	Petit-Mont	F6	limestone	mud mound	below FWWB	
			lateral facies	F5	shaly limestone	no	below FWWB	
		Grand Breux	Boussu-en-Fagnes		shale	no	below FWWB	
			Lion	F4	limestone	mud mound	below FWWB	
			Bieumont	F3	limestone	no	below FWWB	
		Moulin Liénaux	Ermitage	F2	shale	no	below FWWB	
			Arche	F1	limestone	mud mound	below FWWB	
Givetian	Boulonnais	Blacourt	Couderousse	G6	limestone	bioherm	upon FWWB	Hubert 2008
			Griset	G5	limestone	bioherm	close FWWB	
	Dinant syncline	Fromelennes		G4	limestone	bioherm	close FWWB	Boulvain et al. 2009
		Terres d’Haurs		G3	limestone-marl	no	close FWWB	Mabille and Boulvain 2008
		Trois-Fontaines		G2	limestone	bioherm	around FWWB and below	
		Hanonet		G1	limestone	bioherm	close FWWB	Mabille and Boulvain 2007b
Eifeilian		X		E4	limestone	bioherm	upon FWWB	Préat et al. 2007
		Jemelle		E3	marl	no	around FWWB and SWB	Mabille and Boulvain 2007a
		Couvin		E2	limestone	bioherm	around FWWB and SWB	
		Eau Noire		E1	calcareous marl	no	around FWWB 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 palaeocological information, we used the Shannon index H of diversity (Shannon and Weaver 1949), based on abundance matrices.

Where S is the number of samples, pi is the taxa i proportion compared to the sum of abundances of all species at a particular sample, ni 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.

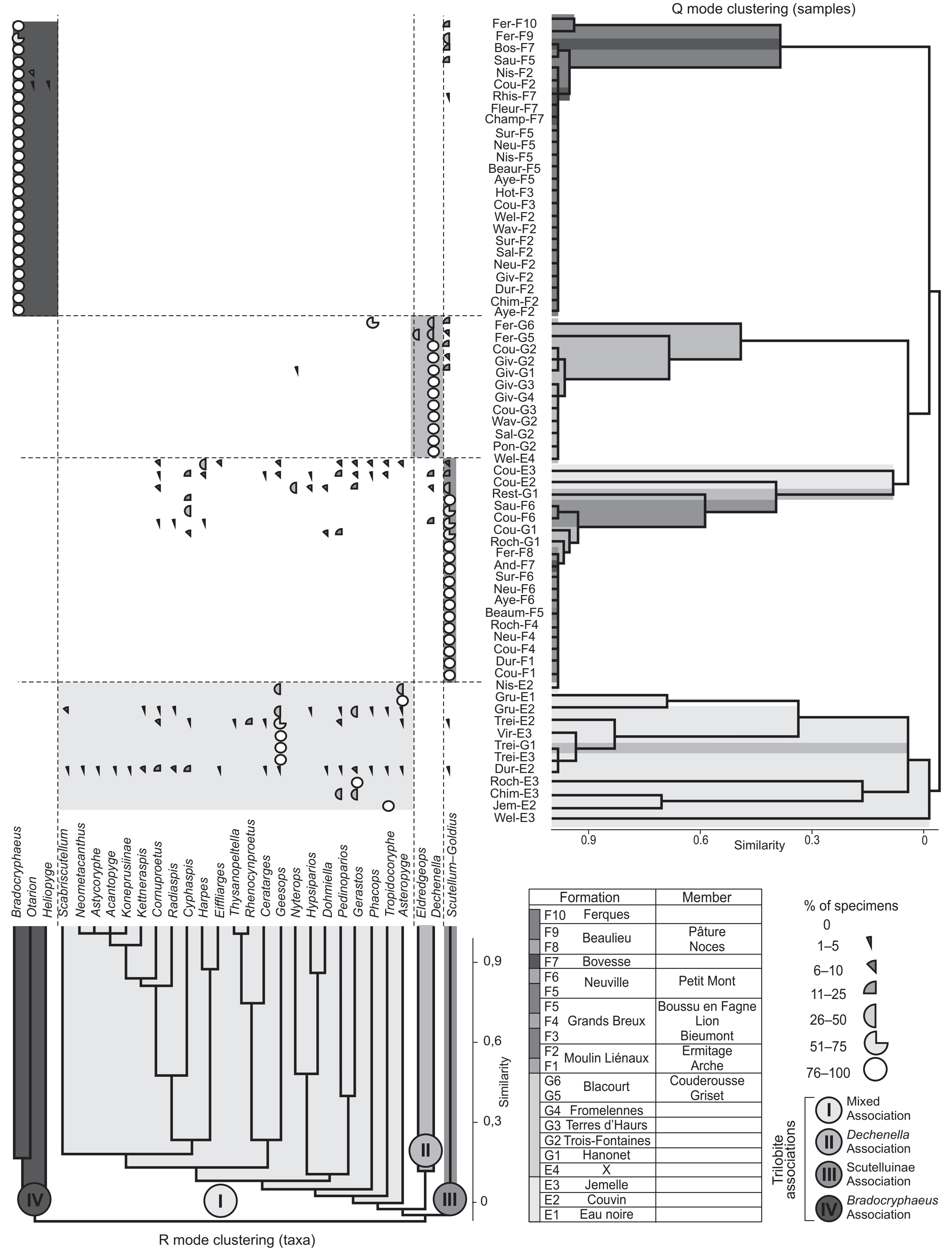
ANOSIM was applied to test for significant differences between the four identified clusters using 5000 permutations and a distance measure (Bray-Curtis index). The R coefficient is 0.847 and the p values is <0.001***, providing a significant difference between taxa groupings and supporting the results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


Q mode clustering (samples)
Fer-F10
Fer-F9
Bos-F7
Sau-F5
Nis-F2
Cou-F2
Rhis-F7
Fleur-F7
Champ-F7
Sur-F5
Neu-F5
Nis-F5
Beaur-F5
Aye-F5
Hot-F3
Cou-F3
Wel-F2
Wav-F2
Sur-F2
Sal-F2
Neu-F2
Giv-F2
Dur-F2
Chim-F2
Aye-F2
Fer-G6
Fer-G5
Cou-G2
Giv-G2
Giv-G1
Giv-G3
Giv-G4
Cou-G3
Wav-G2
Sal-G2
Pon-G2
Wel-E4
Cou-E3
Cou-E2
Rest-G1
Sau-F6
Cou-F6
Cou-G1
Roch-G1
Fer-F8
And-F7
Sur-F6
Neu-F6
Aye-F6
Beaum-F5
Roch-F4
Neu-F4
Cou-F4
Dur-F1
Cou-F1
Nis-E2
Gru-E1
Gru-E2
Trei-E2
Vir-E3
Trei-G1
Trei-E3
Dur-E2
Roch-E3
Chim-E3
Jem-E2
Wel-E3
0.9
0.6
0.3
0
Similarity
Bradocryphaeus
Otarion
Heliopyge
Scabriscutellum
Neometacanthus
Astycoryphe
Acantopyge
Koneprusiinae
Kettneraspis
Cornuproetus
Radiaspis
Cyphaspis
Harpes
Eifliarges
Thysanopeltella
Rhenocynproetus
Ceratarges
Geesops
Nyterops
Hypsiparios
Dohmiella
Pedinoparios
Gerastos
Phacops
Tropidocoryphe
Asteropyge
Eldredgeops
Dechenella
Scutellum–Goldius
0,9
0,6
0,3
0
Similarity
IV
I
II
III
R mode clustering (taxa)
Formation
Member
F10 Ferques
F9 F8 Beaulieu
Pâture Noces
F7 Bovesse
F6 F5 Neuville
Petit Mont
F5 F4 F3 Grands Breux
Boussu en Fagne Lion Bieumont
F2 F1 Moulin Liénaux
Ermitage Arche
G6 G5 Blacourt
Couderousse Griset
G4 Fromelennes
G3 Terres d'Haurs
G2 Trois-Fontaines
G1 Hanonet
E4 X
E3 Jemelle
E2 Couvin
E1 Eau noire
% of specimens
0
1–5
6–10
11–25
26–50
51–75
76–100
Trilobite associations
I Mixed Association
II Dechenella Association
III Scutelluinae Association
IV Bradocryphaeus Association

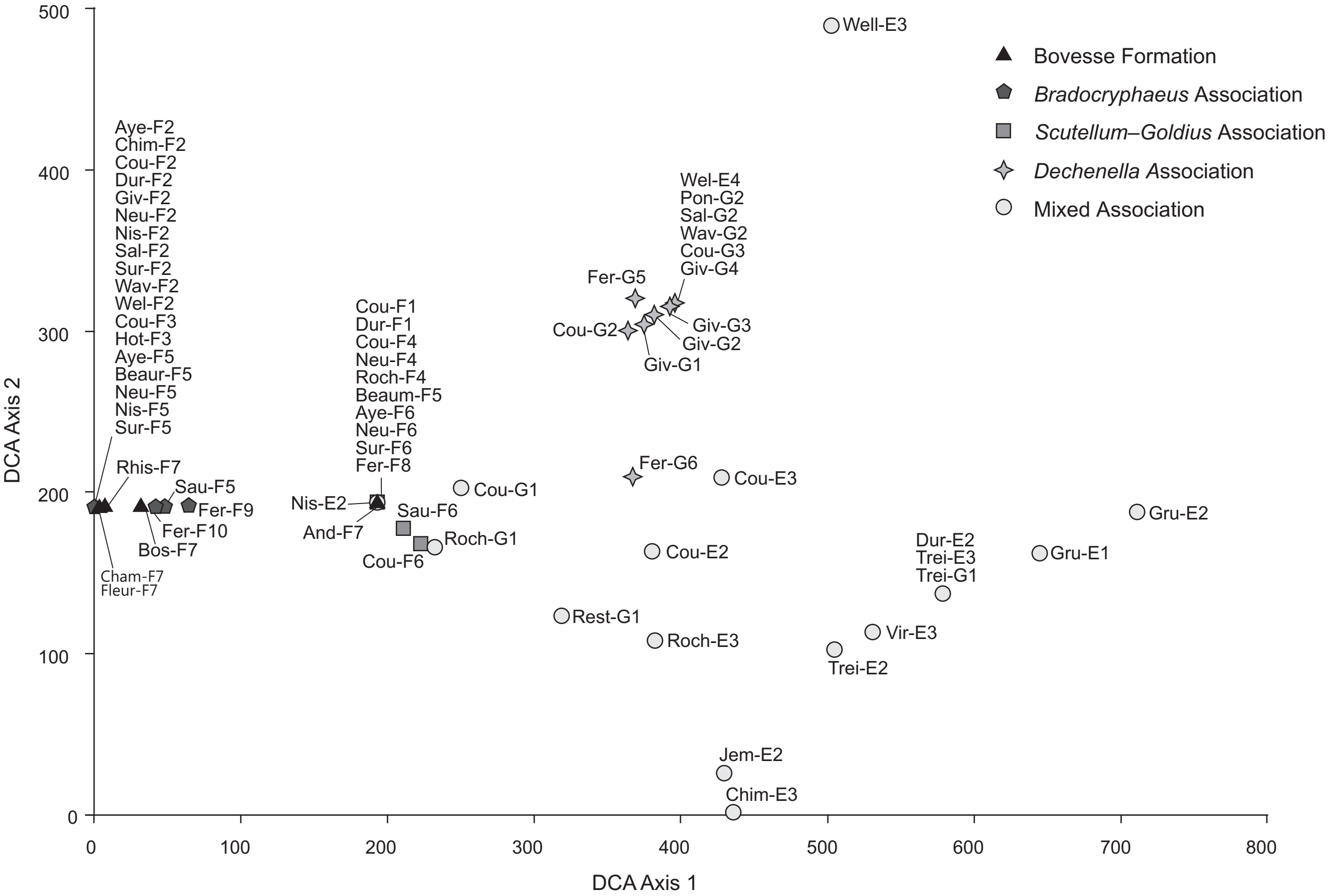


Fig. 4. Scatter plot of 29 trilobite taxa for 67 samples from the Middle and Upper Devonian of the Ardenne Massif and Boulonnais (France, Belgium), according to DCA (see Fig. 2, 3 for abbreviations). The two first axes represent respectively 42.8 and 28.1% of the total variance.

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. Dendogram 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, Beauraing; 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, Resteigne; 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.

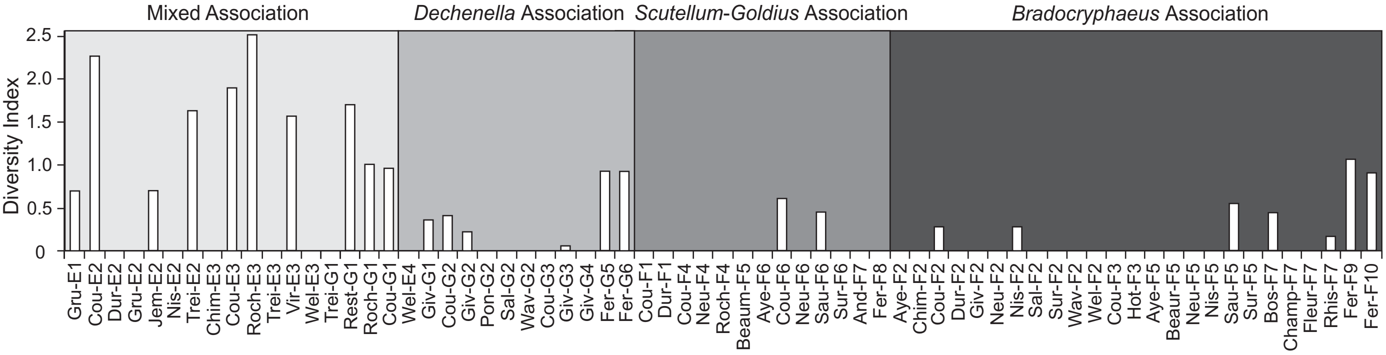


Fig. 5. Diversity (Shannon-Weaver index) of the 67 trilobites samples from the Middle and Upper Devonian of the Ardenne Massif and Boulonnais (North France, Belgium) for four delineated associations (see Figs. 2, 3 for abbreviations).

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 Beaulieu 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 Pâture Member of the Beaulieu 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 (Paterson 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 commonly 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-preserved deposit called the “Mur des douaniers” in Vireux-Molhain (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 (Crônier 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 index 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 transport, with fauna contamination between the different formations (or members) for both spatially and temporally being unlikely. However, diagenesis and tectonic conditions have reduced the biodiversity of a significant portion of the sections 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 “impact” on the trilobite benthic association. Indeed, the Mixed association flourishes on the median ramp (Eau Noire and Jemelle formations; Bultynck and Dejonghe 2001; Dumoulin and Blockmans 2008; Fig. 6A) and on a barrier locally developed (Couvin Formation; Mabille and Boulvain 2007a; Fig. 6B). The trilobites are constrained to forereef environments at a similar depth as the median ramp facies. No correlation 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)

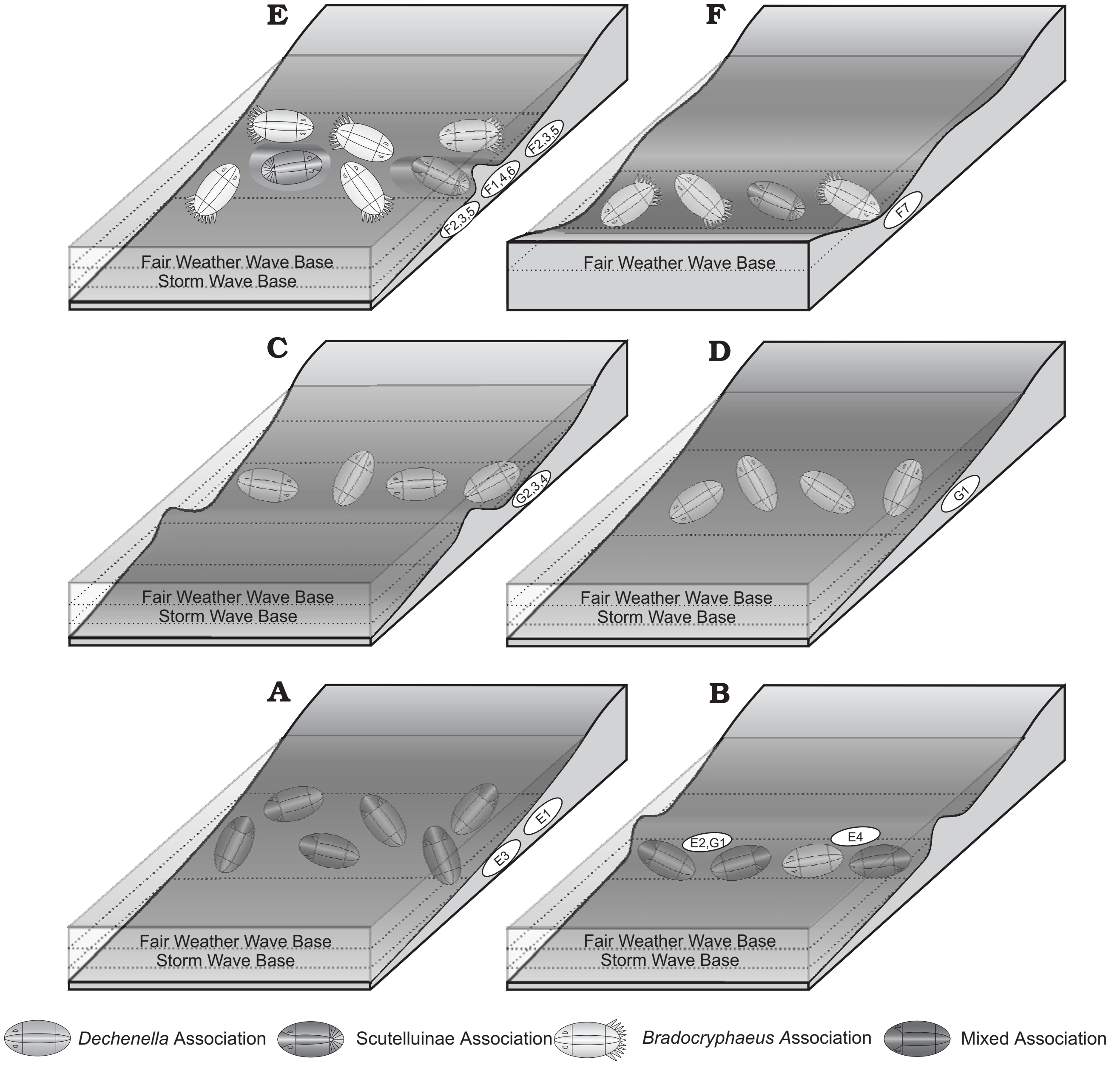


Fig. 6. Distribution of trilobite associations in the southern border of Dinant synclinorium, Ardenne Massif (Belgium, France) during the Middle and Late Devonian (see Fig. 2 for abbreviations). **A**. Eifelian ramp. **B**. Eifelian reef. **C**. Givetian carbonated platform. **D**. Givetian ramp. **E**. 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'Haurs, 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, FWWB 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 FWWB (within Griset 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-

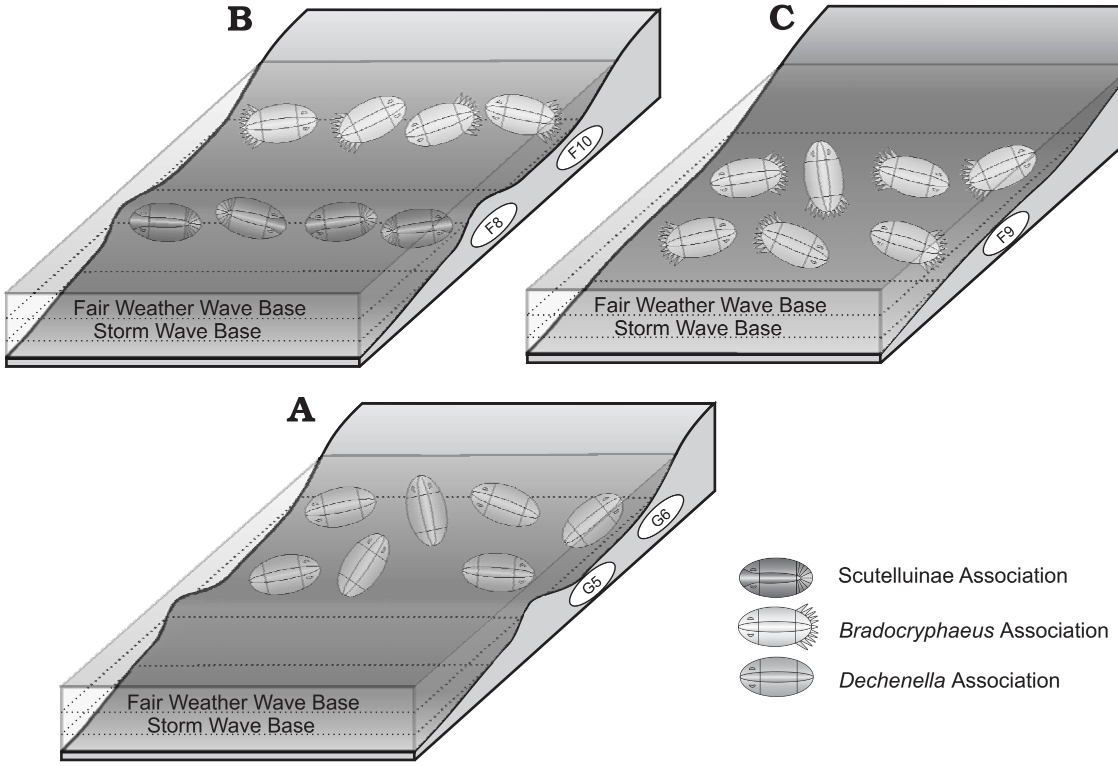


Fig. 7. Distribution of trilobite associations in the Boulonnais (North of France) during the Middle and Upper Devonian (see Fig. 2 for abbreviations). **A**. Givetian carbonated platform. **B**. Frasnian platform. **C**. Frasnian shaly facies.

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 Pâture 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 Asteropyginae, in reef facies and the clastic shelf of the Nocedo Formation. Nevertheless, a posterior conodont study (Keller and Grötsch 1990) attributed a Givetian age to the Nocedo 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 Préat 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.

Acknowledgements

The authors thank Annelise Folie (Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium) who kindly offered access to her collection. The manuscript benefited from constructive review made by Melanie Hopkins (American Museum of Natural History, New York, USA) and Raimund Feist (Université de Montpellier, Montpellier, France). We greatly appreciate the English corrections of Jane Hall (Yale University, New Haven, USA). This study was supported by the Synthesys Project (http://www.synthesys.info) which is funded by the European Community Research Infrastructure Action under the FP6 "Structuring the European Research Area Programme". This paper is a contribution to UMR Géosystèmes-CNRS and to IGCP 596 "Climate change and biodiversity patterns in the mid-Palaeozoic".

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