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Stromatoporoid diversity in the Devonian of the Ardennes: a reinterpretation

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ABSTRACT. Previous studies of the stromatoporoid palaeobiodiversity in the Devonian of the Ardennes are revised. The data set used in this study consists of 3416 specimens of 180 species. The rarefaction method was employed in order to reduce sampling bias in the diversity curves. The estimated stromatoporoid diversity reached its plateau in the Eifelian (Couvin Formation) and in the Givetian, and decreased during the Late Devonian.

KEYWORDS: stromatoporoids, palaeobiodiversity, Eifelian, rarefaction, diversity curves

1. Introduction

Devonian stromatoporoids (class Stromatoporoidea Nicholson & Murie, 1878) of the Ardennes and adjacent areas have been extensively studied for the last 80 years, beginning from the pioneer works by Le Maître (1931, 1933) and Lecompte (1951, 1952), to the recent contributions by Mistiaen (2002), Hubert (2008) and Da Silva et al. (2011). Givetian and Frasnian stromatoporoid faunas received the most extensive scientific attention (e.g. Lecompte 1951, 1952; Cornet, 1975), but Emsian, Eifelian and Famennian stromatoporoids were also described (e.g. Conil, 1960; Bultynck, 1970). Most of the studied specimens were collected from the southern border of the Dinant Synclinorium (Fig. 1). Stromatoporoids from the Namur Synclinorium, the Vesdre area, western Germany and the Boulonnais were also studied (e.g. Mistiaen, 1980, 1988, 2002; Flügel, 1974). Recent years have witnessed a shift toward palaeobiodiversity studies (e.g. Hubert et al., 2007).

Previous research on the diversity of stromatoporoids in the Devonian of the Ardennes revealed a single diversity peak in the Givetian (Blieck et al., 2006; Hubert et al., 2007; Zapalski et al., 2007). Abundance, measured at the species level, rose significantly in the Eifelian and the Givetian and dropped in the Frasnian and the Famennian. Species richness in the Eifelian was nearly three times lower than in the Givetian (Blieck et al., 2006). Such results differ from the global diversity patterns. Stock (2005a, 2005b) estimated that at the global scale and at the genus level stromatoporoid diversity reached a peak in the Eifelian. The current study discusses the differences between global and local patterns by examining possible sources of bias that influence biodiversity estimations.

The stromatoporoid palaeobiodiversity curve generated by Hubert et al. (2007) reveals a significant positive correlation with the presence of biostromes and carbonate facies. Such a finding is not unusual since poor environmental conditions could result in a lower number of taxa. On the other hand the lack of numerous easily accessible outcrops of biostromes containing abundant stromatoporoids may also lead to a further underestimation of the biodiversity documented in the fossil record, since poorly exposed sedimentary rocks are sampled less intensively (Peters & Foote, 2001). Raup (1976a, 1976b) concluded that diversity trends and rock outcrop area are linked. Other studies (e.g. Miller & Foote, 1996) revealed that sampling problems indeed affect biodiversity curves. Raw diversity trends, such as those presented by Hubert et al. (2007), should therefore be supplemented by analyses that allow evaluation of the effects of sample size on observed species richness.

Results of such analyses are discussed in the present contribution. In order to evaluate the effects of sample size on the stromatoporoid diversity in the Devonian of the Ardennes, the rarefaction method was employed (Sanders, 1968; Raup, 1975). It allows to determine whether the number of taxa reflects the real biodiversity or whether it is an artifact caused by unequal sample sizes. The rarefaction method was not used in the previous estimations of palaeobiodiversity in the Devonian of the Ardennes (Hubert et al., 2007; Zapalski et al., 2007).

2. Material and methods

The data set employed in this study is the result of an extensive literature survey. Both published papers and unpublished dissertations/theses devoted to Devonian stromatoporoids from Belgium and France (Avesnois; Fromelennes near Givet) were used. The collections are listed in Table 1. A similar database was compiled by Hubert et al. (2007); however, the data used in the study was not corrected for sample size. Occurrences from the Devonian of the Boulonnais (Mistiaen 1980, 1988, 2002) and Germany (Paul, 1939; Flügel, 1974;

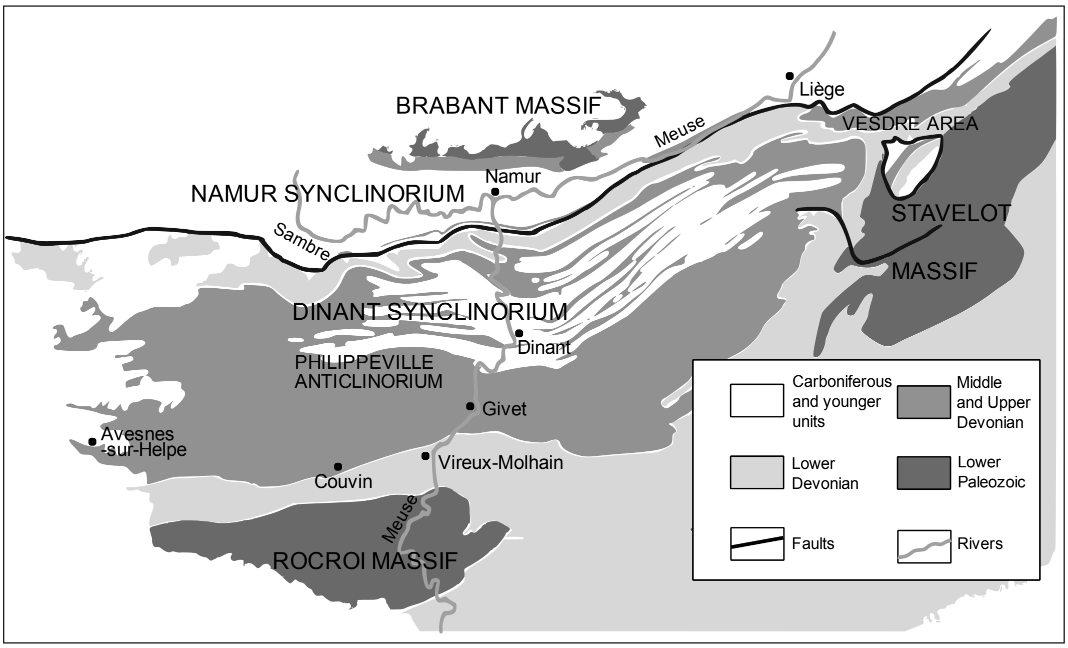

Figure 1. Schematic geological map showing the distribution of the Devonian outcrops in the Ardennes (modified from Bultynck & Dejonghe, 2001).

Author	Number of specimens used in this study	Number of species	Age	Location
Bultynck, 1970	29	21	Emsian, Eifelian	SBDS
Conil, 1960	21	10	Famennian	Dinant Synclinorium, VA
Cornet, 1975	2145	84	Givetian, Frasnian	SBDS, Philippeville Anticlinorium
Hubert, 2008	387	55	Givetian	SBDS
Lecompte 1951, 1952	693	108	Eifelian, Givetian, Frasnian	Dinant Synclinorium
Le Maître, 1933	27	12	Famennian	Avesnois
Mistiaen, 1997	80	1	Famennian	Avesnois
Mistiaen, 2007	1	1	Emsian	Vireux-Molhain (France)
Rensonnet, 2005	31	13	Frasnian	VA
Weber, 1999	2	1	Famennian	VA

Table 1. Stromatoporoid collections used in the present study. Explanation of abbreviations used: SBDS – southern border of the Dinant Synclinorium, VA – Vesdre area, Avesnois – localities in the vicinity of Avesnes-sur-Helpe, Northern France.

Flügel & Flügel-Kahler, 1975; Weber, 1999; Weber & Mistiaen, 2001; Mistiaen & Weyer, 2007) were excluded from the study, except for two specimens described by Weber (1999) which were from the Uppermost Famennian of Belgium. The database prepared for the present analysis contains a total of 3416 specimens and 180 species. The exact number of specimens studied by Lecompte (1951, 1952) was not available due to the lack of data in the published monograph. A number of type specimens of each species and a number of localities were therefore used. Diversity was estimated at the species level. However, the genus-level data are considered as being more taxonomically robust (Alroy, 1996). Generic attributions of the species under study were not revised since the biodiversity was estimated at the species level. All subsequent workers followed taxonomic definitions introduced by Lecompte (1951, 1952) and Le Maître

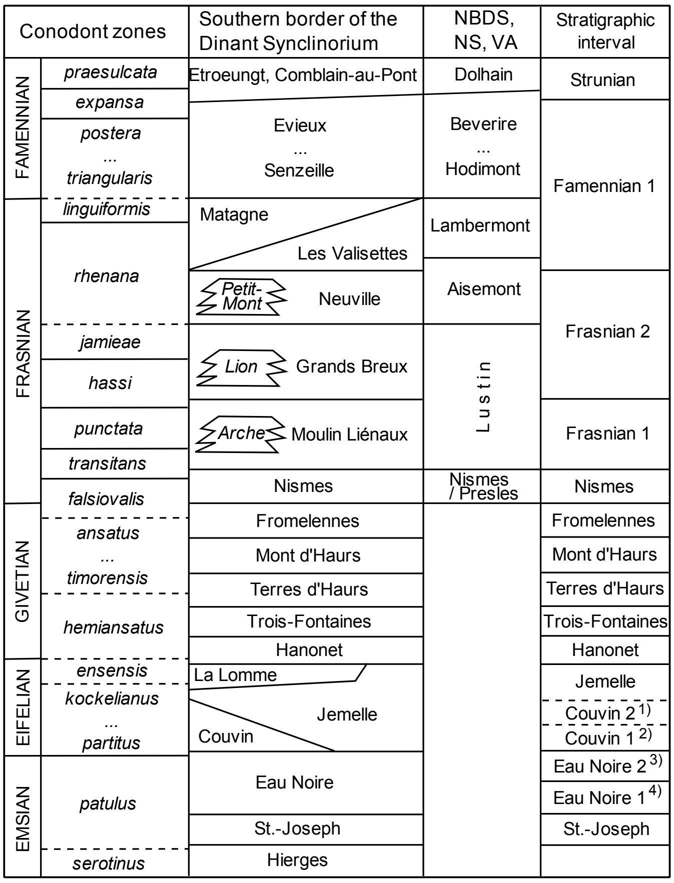

Figure 2. Emsian to Famennian (Devonian) lithostratigraphic units of the Ardennes and stratigraphic intervals used in this work. The conodont zonation (after Bultynck & Dejonghe, 2001) refers to the southern border of the Dinant Synclinorium. Explanation of abbreviations and symbols used: NBDS – northern border of the Dinant Synclinorium, NS – Namur Synclinorium, VA – Vesdre area, 1) – Co2b in the former stratigraphic subdivision (Maillieux & Demanet, 1929), 2) – Co2a, 3) – Co1c, 4) – Co1b.

(1933), although some species were transferred to other genera (synonymic lists were published by Hubert et al., 2007). Thus it is unlikely that inconsistencies in taxonomy, such as those noticed previously by Patterson & Smith (1987), could affect the results of the present study.

Stromatoporoid diversity was computed by creating composite faunal lists for 16 stratigraphic units, summarized in Fig. 2. The exact stratigraphic position of each unit was estimated using the current lithostratigraphic division of the Devonian of Ardennes (Bultynck & Dejonghe, 2001). Stratigraphic attributions in papers that used the former stratigraphic subdivision of the Devonian of the Ardennes, introduced by Maillieux & Demanet (1929), were corrected. Specimens of unknown age (chiefly from Lecompte's collection) were excluded from the study.

In the previous studies stromatoporoid faunas were analysed stage by stage. Time intervals recognized in this paper have shorter durations than stages, and thus are less prone to error caused by different time spans of specific stages, and changes of boundaries over time (Hubert et al., 2007). Lithostratigraphic units however tend to be diachronous. Additionally, the duration of intervals defined using stratigraphic subdivisions is not equal. Better results than those obtained in the present study could be achieved if the traditional time scale is abandoned and the diversity curve is computed directly from the faunal lists (Alroy, 1996); this method is, however, best suited for studies of the more recent (Cenozoic) fossil record. In the present study stratigraphic units were therefore used.

Species richness increases with sample size (Oksanen et al., 2010). Thus, differences in species richness estimated from the raw data may be at least partially caused by the differences in the number of specimens sampled from each interval. A way to remove such bias is to rarefy the number of specimens in each sampling interval to a similar level, using the rarefaction method (Sanders, 1968; Raup, 1975). The number of specimens in each interval should be rarefied to the level recorded for the time span with the smallest sample size. However, in this study, sample size differs from 0 to 1396. Thus, in order to preserve as much data as possible, the appropriate number of species occurrences should be larger than the smallest sample size. An arbitrary sampling level had to be chosen, and intervals that were under-represented at this level were excluded from further analyses. Rarefied species richness was estimated at a sample size of 24 specimens. The expected number of species in a community rarefied to 24 individuals could not be determined for six intervals from which fewer stromatoporoid specimens were sampled.

In addition to standard biodiversity curves obtained from the raw and rarefied data, rarefaction curves were also plotted. Their shapes are determined by the observed number of species, the number of specimens, species frequency and the number of specimens per species (Foote, 1975). Rarefaction curves allow diversities calculated from many intervals to be compared readily. Conclusions drawn from these curves are relatively independent of sample size.

The expected species richness in random subsamples of unified sizes was estimated using the R Project for Statistical Computing (R Development Core Team, 2009) and the 'rarefy' function in the 'vegan' package (Oksanen et al., 2010). The rarefied diversity is calculated as described by Hurlbert (1971). Formulae for computing the standard errors are based on Heck et al. (1975). Rarefaction curves were calculated and interpreted according to Miller & Foote (1996).

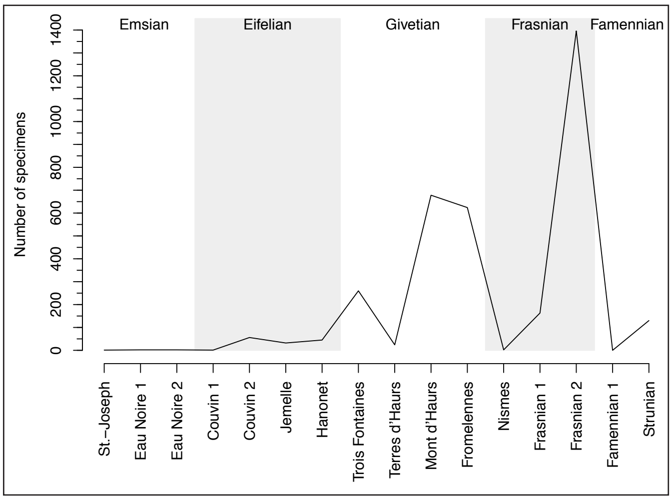

Figure 3. Number of specimens from each stratigraphic interval.

3. Results and discussion

The data used in this study show dramatic sampling peaks in the Givetian (Trois-Fontaines and Mont d'Haurs Formations) and in the Frasnian (Fig. 3). The number of specimens is correlated with carbonate facies distribution. The accessibility of the outcrops is also important. The Arche Member of the Moulin Lienaux Formation (Frasnian 1 interval), which was not mined in the La Boverie quarry in the 1970s when Devonian stromatoporoids were studied by Cornet (1975), is significantly less sampled. Moreover, the Eifelian and Famennian data are absent from certain large collections used in this study (Table 1). This suggests that the differences in species richness may be partially caused by differences in sample size. Apart from a standard biodiversity curve of the raw data (Fig. 4), a curve based on rarefaction estimates was thus plotted (Fig. 5). Both curves differ for at least two stratigraphic intervals used in this study: the Couvin 2 and Trois-Fontaines Formation. In order to identify possible sources of these differences, rarefaction curves were also calculated (Fig. 6).

The biodiversity curve of the raw data (Fig. 4) reveals distinct peaks in the observed number of species and roughly follows the trajectory shown in Fig. 3. The highest diversity is observed during the Givetian and the Frasnian. Stromatoporoid diversity at the species level is similar to that estimated by Hubert et al. (2007), except for the peak in the Frasnian 2 interval. This distinct peak may be an artifact of the extraordinarily large number of specimens sampled from this interval and the different time spans used in both studies. Moreover, Hubert et al. (2007) omitted the collection by Rensonnet (2005), which includes specimens from the Frasnian. Both curves reveal relatively low diversity during the Eifelian.

The Devonian diversity trajectory based on rarefaction estimates is presented in Fig. 5. The rarefied diversity curve reveals no clear peak. Stromatoporoid biodiversity increased abruptly in the Eifelian (Couvin 2), when carbonate facies became established in the Ardennes. The number of species decreased after the Givetian (in the Frasnian 1 stratigraphic interval). A further decrease in stromatoporoid biodiversity was recorded in the Strunian stratigraphic interval.

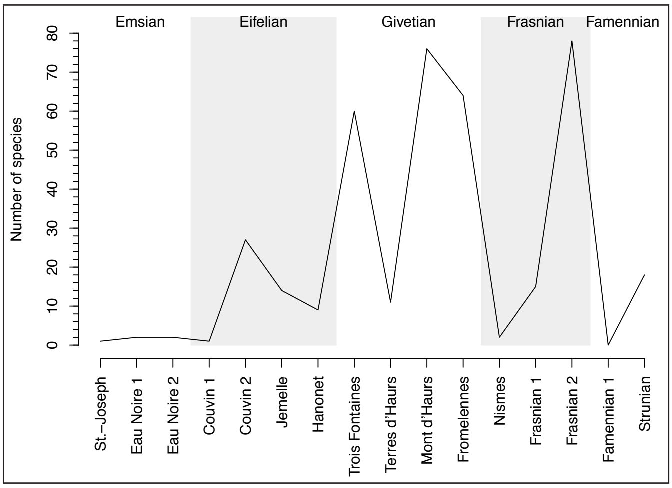

Figure 4. Species-level stromatoporoid diversity through the Devonian, for each stratigraphic interval defined in Fig. 2 (from the Emsian to the Famennian), calculated from raw data.

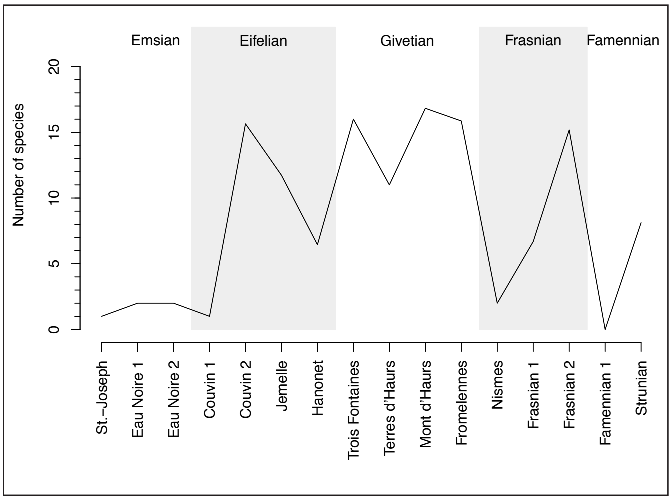

Figure 5. Devonian diversity curve based on rarefaction estimates of species richness at a sample size of 24 occurrences. A diversity curve is plotted for all stratigraphic intervals, but stratigraphic intervals with a small number of specimens (fewer than 24; St. Joseph to Couvin 1, Nismes and Famennian 1) were omitted from the interpretation of results.

The most striking feature of this curve is the very high stromatoporoid diversity in the Lower Eifelian (Couvin Formation). This indicates that a plateau in diversity was reached shortly after carbonate facies became established in the studied area.

Another important feature of the rarefied diversity curve is high stromatoporoid biodiversity in the Frasnian 2 stratigraphic interval (Grands Breux and Neuville Formations; upper part of the Lustin Formation). This phenomenon could potentially result from either the longer duration of this interval (from the *hassi* to the Lower *rhenana* conodont Zone) or more pronounced facies differences, since stromatoporoids were described both from the southern and northern borders of the Dinant Synclinorium, from the southern part of the Namur Synclinorium and from the Vesdre area, contrary to the preceding time intervals. However, most of the biodiversity recorded for this interval is concentrated within the Lion Member of the Grands Breux Formation. Differences in sample sizes (nearly 1/3 of all the specimens in the studied collections were sampled from this single stratigraphic interval) were corrected using the rarefaction method, and thus cannot be considered as an explanation for the high biodiversity. Stromatoporoids from the Frasnian 1 stratigraphic interval exhibit significantly lower species richness than those in the Trois-Fontaines and Mont d'Haurs Formations, which follows the conclusions of previous workers (Hubert et al., 2007). However, in their study stage-level intervals were used.

Rarefaction curves for 10 time spans from which at least 24 stromatoporoid specimens were collected are presented in Fig. 6. The Couvin 2 curve lies slightly below the Trois-Fontaines and Mont d'Haurs Formations curves. It indicates that, after adjusting for sample size differences, stromatoporoid diversity could have reached its plateau during the Eifelian. Thus, although in the Eifelian environmental conditions were less favourable for stromatoporoid growth than in the Givetian, the relatively low number of species described from the Couvin Formation (Lecompte 1951, 1952; Hubert et al., 2007) could be an artifact of sampling.

Diversity curves obtained for the Jemelle and Terres d'Haurs Formations are steep, showing a relatively low specimen/species ratio. This suggests that palaeobiodiversity at the species level could be significantly higher; however, such statements have to be treated with care, since rarefaction curves should not be extrapolated beyond their endpoints (Miller & Foote, 1996). Moreover, both formations are characterized by opportunistic species and by limited stromatoporoid biodiversity.

In the Latest Famennian (Strunian) stromatoporoids were still well diversified. The rarefaction curve (Fig. 6B) plotted for this

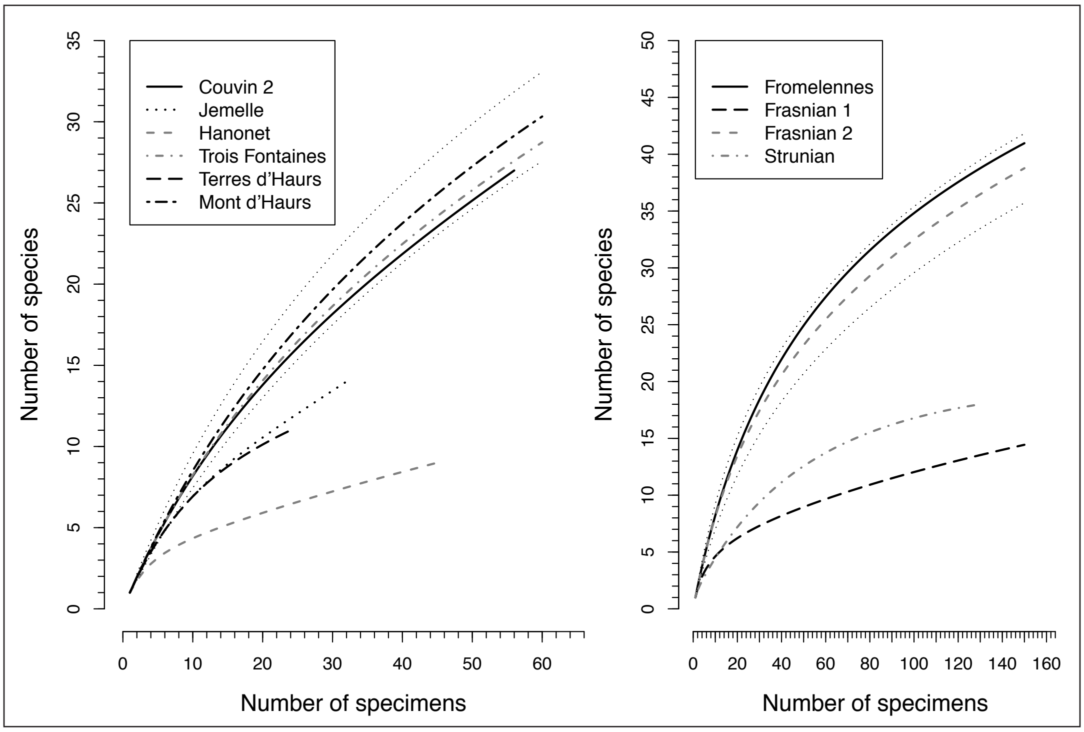

Figure 6. Comparative rarefaction curves for 10 stratigraphic intervals with more than 23 specimens. Dotted lines depict standard error around the curves for the Mont d'Haurs Formation (graph on the left) and Frasnian 2 stratigraphic interval (graph on the right). Standard errors computed for other curves are lower, and confidence bands are thus omitted to avoid obscuring the curves.

stratigraphic interval virtually coincides with the curve obtained for the Lower and Middle Frasnian (Moulin Liénaux Formation).

Future studies should investigate other factors that could affect palaeobiodivesity estimation, namely incorrect or obsolete species diagnoses. Some stromatoporoid species established by Lecompte (1951, 1952) were synonymized with one another by later workers (e.g. Kaźmierczak, 1971). Such synonymies are not reflected in the present study.

Similar analyses employing the rarefaction method could be also undertaken at the genus level. This implies, however, that attributions of species to genera have to be revised, in order to make sure that inconsistencies in taxonomy, such as those noticed by Patterson & Smith (1987), will not affect the results. Some of the stromatoporoid species established by Lecompte were re-described by later authors (for detailed information, see Hubert et al., 2007). Other species still need to be revised. Future research might also examine stromatoporoid collections from the Boulonnais and western Germany. Another improvement in the results could be achieved by performing rarefaction analysis of morphological variety (Foote, 1992).

4. Conclusions

Rarefied data reveal that a plateau in stromatoporoid diversity was reached in the Eifelian, shortly after carbonate facies became established in the Ardennes. The estimated palaeobiodiversity declined in the Frasnian. However, in the Middle and Late Frasnian stromatoporoids were still well diversified. This phenomenon could potentially result from the longer duration of this interval. Stromatoporoid diversities in the Early and Middle Frasnian (Moulin Liénaux Formation) and in the Latest Famennian (Strunian) were comparable.

Results obtained during the present study are consistent with conclusions reached by Stock (2005a, 2005b) on a global scale. A peak of stromatoporoid diversity in the Eifelian (Couvin Formation) was not recognized in the Devonian of the Ardennes by the previous researchers due to undersampling.

Future estimations of stromatoporoid palaeobiodiversity in the Devonian of the Ardennes should take into account a possible bias caused by uneven sample sizes. The rarefaction method allows such bias to be removed. The durations of time intervals used in further studies should be similar.

5. Acknowledgements

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