

A 12- to 14-million year faunal diversity cycle in the Ordovician of Western Baltica

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Hammer, Ø.: A 12- to 14-million year faunal diversity cycle in the Ordovician of Western Baltica. *Norwegian Journal of Geology*, Vol. 83, pp. 79-84. Trondheim 2003. ISSN 029-196X.

The faunal (all fossil groups) species diversity curve for the Ordovician of Norway shows a strong and statistically significant cycle with a period of 12 to 14 million years. The cycle is supported by spectral analysis, autocorrelation and wavelet analysis. A spectral peak for a similar periodicity can also be seen in the diversity curve from Swedish collections, but is not statistically significant. The number of preserved species may be partly a reflection of differences in primary alpha diversity and differential preservation at different water depth. The causal mechanism for this periodicity is a matter of speculation, but may be sought in processes such as periodic tectonic or volcanic activity, or climate change by astronomical forcing.

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Introduction

Possible periodicity in global faunal and floral diversity patterns has been a much debated issue since the 'Nemesis' hypothesis of Sepkoski & Raup (1986). Their putative 26-million years periodic extinction cycle in the post-Palaeozoic has been much criticised on statistical grounds (Hoffmann 1989; Benton 1995), but has also received substantial support from analysis of other data sets (Hart 1990; Rampino & Caldeira 1992; Prokoph et al. 2000). Several of these studies indicate a somewhat longer cycle of about 30 million years. The mechanism for such periodicity, if it at all exists, is unknown, and suggestions have ranged from bolide impacts (Rampino & Stothers 1986), flood basalt events (Stothers 1993; Yabushita 1998) and magnetic field reversals (Stothers 1986) to sea level change (Hallam 1989; Hart 1990) and purely 'intrinsic' ecological processes (Bak 1997).

The possibility of periodicity in biodiversity and extinction patterns in the Palaeozoic has been investigated much less intensely. A clear cycle with a 12 to 14 million year periodicity in diversity counts can be detected in the Ordovician of Norway and to a smaller extent Sweden, corresponding to the western limits of the small palaeo-continent of Baltica.

Such a local study will always be strongly influenced by insufficient preservation and sampling, but it is believed that southern and western Scandinavia, as a whole, represents a relatively complete stratigraphical record through the Ordovician. More or less randomly distributed local hiatuses are common, but are not expected

to produce false features in the diversity curves. Of greater concern are the larger-scale unconformities as described by e.g. Dronov and Holmer (1999), including in the uppermost Pakerort, uppermost Billingen, uppermost Kunda, Oandu and Nabala stages of Sweden.

High-resolution time series analysis of diversity patterns may also be easier to carry out with a data set of limited geographical extent, because biogeographical heterogeneity can otherwise obscure temporal patterns. Stratigraphical correlation is also less prone to error over relatively short distances. In the Lower and Middle Ordovician of Scandinavia it appears that cyclicity is more pronounced in generally more deep-water localities (Norway vs. Sweden), indicating that these communities were more sensitive to the environmental or ecological factors driving the cycle.

Material

The data were taken from a database of more than 10,000 records of published first and last appearance data (FADs and LADs) of species from all fossil groups in the Ordovician of Baltoscandia, with separate records for different localities. The data were taken from 141 publications, ranging from records of a single taxon to large faunal compilations. Taxonomic standardization was attempted using recent literature. The database itself and a list of the publications used are available at the web page asaphus.uio.no. The FADs and LADs were converted to approximate apparent ages using the age model of Cooper (1999) and Webby et al. (in press), as shown in Fig. 1. There are relatively few

Ma	GLOBAL SERIES	GLOBAL STAGE	BRITISH SERIES	BALTO-SCANDIAN SERIES	BALTO-SCANDIAN STAGE
440					
450	Upper Ordovician		Ashgill	Harju	Porkuni Pirgu Vormsi Nabala
460			Caradoc	Viru	Rakvere Qaidu Keila Johvi Idavere Kukruse Uhaku
470	Middle Ordovician	Darriwilian	Llanvirn	Kunda	Aseri Aluoja Hunderum Langevoja
480	Lower Ordovician		Arenig	Volkhov	Billingen
				Latorp	Hunneberg
490		Tremadocian	Tremadocian		

Fig. 1. Chronostratigraphical scale used in this study, based on Cooper (1999) and Webby et al. (in press).

good radiometric dates available that can be accurately placed within the biozonation. Cooper (1999) interpolated the radiometric dates using biostratigraphic event spacing in pelagic sequences where sedimentation rate is assumed to be relatively constant. The approximate absolute ages used in this study have errors caused by a number of inaccuracies: errors in radiometric dates, errors in the relative time scale used by Cooper and departures from constant sedimentation rates in his pelagic sequences, and errors in the correlation of Baltoscandian bio-events, stage, zone and lithological boundaries with the zones used by Cooper (a list of the correlations used is given at the web page). These errors should be kept in mind when assessing the significance of detected cyclicities. In addition, a subtle question of possible statistical dependency between diversity and time is raised by the fact that Cooper used Baltoscandian graptolite data as part of the basis for his time scale. However, such effects are likely to be weak.

Mean standing diversities in 1-million year time slices were estimated by letting species ranging through a time slice count as one unit in that slice, while species with their FAD or LAD in a time slice contribute a half unit in that slice. Species that only exist within one time slice count a third of a unit. This method aims to reduce artificial inflation of taxonomic richness in intervals with high turnover rates. More detailed description of the database and the methods for estimating diversity, together with diversity curves and randomisation tests, are given by Hammer (in press).

Methods

The most common method for detecting periodicity in time series is spectral analysis, resulting in a spectrogram where 'power' (squared amplitude) is plotted as a function of frequency, i.e. number of cycles per time unit. Strong periodicities will appear as peaks in the spectrum (Press et al. 1992; Muller & MacDonald 2000; Proakis & Manolakis 1992; Prokoph et al. 2000). The spectral analysis was carried out as follows. A few data points at the base and top of the Ordovician were removed as these may be artificially depressed due to missing counts of Lazarus taxa (edge effect). The curves were then detrended by subtracting the straight line obtained by linear regression. This is done in order to remove the increasing trend of the curves, which could otherwise obscure pattern in the spectrograms. Power spectra were estimated using the Lomb periodogram method (Press et al. 1992). For evenly spaced data, this algorithm gives results comparable to the Discrete Fourier Transform (Proakis & Manolakis 1992). An estimate of the white noise floor was calculated, allowing a test of statistical significance (Press et al. 1992). Another, more informal test was carried out by random reshuffling of the data points, keeping their statistical distribution but removing their temporal relations. The powers of the spectral peaks of the randomised signal were then compared to the powers of the peaks from the original sequence.

Wavelet analysis can highlight periodicities, and also allows the study of non-stationary time series where periodicity changes through time (e.g. Prokoph et al. 2000). The quasi-continuous wavelet transform with the Morlet wavelet basis (Grossman & Morlet 1984) was used, allowing high-resolution study of the time series at large and small scales. The result of the analysis is presented in a scalogram, which is a diagram with time along the horizontal axis and the logarithm of scale along the vertical axis. Strength of the signal at any particular time and scale, that is, degree of correlation with the scaled and translated wavelets, is shown using a greyscale. Long-term (large scale) features can then be read along the top of the diagram, while short-term details (small scale) can be read along the bottom.

Autocorrelation (e.g. Davis 1986) proceeds by correlating the time series with a copy positioned at progressively increasing time delays (lag times). The correlation coefficient as a function of lag time will show a distinct peak at lag times corresponding to periodicities in the signal, also for non-sinusoidal components.

The time series was trimmed and detrended as described above also prior to wavelet analysis and autocorrelation.

All data analysis was carried out in the software package PAST (Hammer et al. 2001).

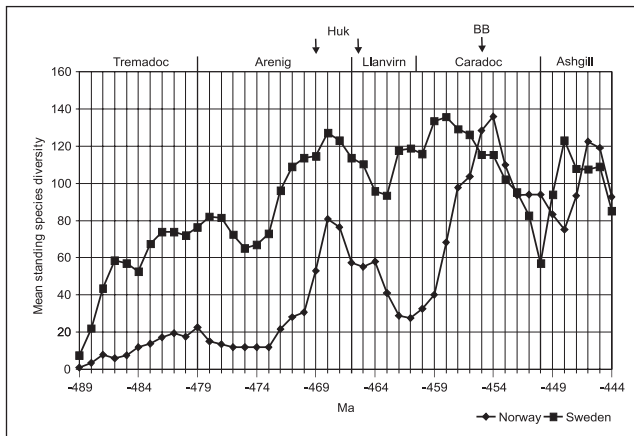


Fig. 2. Mean standing diversity at the species level for all fossil groups in the Ordovician of Norway (diamonds) and Sweden (squares). Three main cycles can be seen in the Norwegian curve, with biodiversity peaks in the late Tremadoc (Bjørkåsholmen to Tøyen Fm.), late Arenig (Huk Fm.) and mid Caradoc. An Ashgill peak occurs somewhat early compared with the apparent periodicity of the first three peaks. Similar but weaker cycles are seen in the Swedish curve.

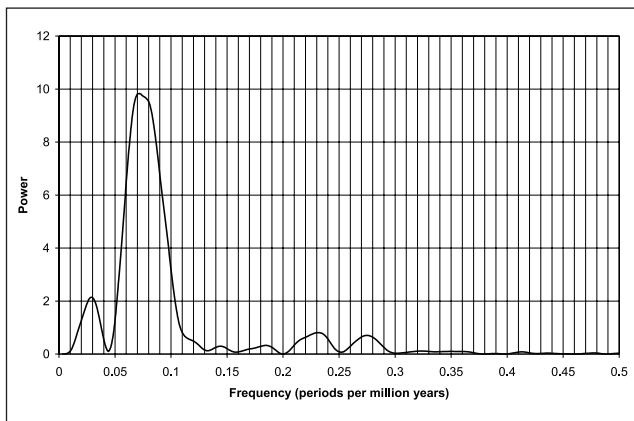


Fig. 3. Spectrogram of the Ordovician diversity curve for Norway, showing a very strong spectral peak for a period of 13.5 million years (0.074 periods per million years). Horizontal axis is frequency (periods per million years), vertical axis is power (square of amplitude in arbitrary units). $p=0.05$ significance level is at a power of 7.5, $p=0.01$ at 9.1.

Results

In the present discussion, Norway and Sweden will be treated separately, allowing an extra test on the robustness of the patterns when only subsets are studied. The two countries have to a large degree been studied by separate research communities, and many parts of the successions comprise different lithologies. The Swedish data are generally taken from localities on the craton, excepting the deeper-water localities in Scania (Jaanusson 1982). The biodiversity curves for Norway and Sweden are given in Fig. 2. A degree of periodicity is indicated already by visual inspection of these curves. Four main cycles can be seen, with peaks in the latest Tremadocian, late Arenig, Caradoc and Ashgill.

The diversity curves can be visually inspected in order to assess informally whether unconformities correlate with important minima in preserved biodiversity. Concentrating first on the Swedish curve, comparing with the stratigraphy given by Dronov and Holmer (1999), the low diversity of the lowermost Tremadocian may be partly due to the lack of preserved sediments. In contrast, the preserved biodiversity minimum of 474-473 Ma (Billingen stage) does not correspond to any unconformity. The hiatus of the uppermost Billingen, at 472 Ma in our time scale, does not correspond to any minimum in preserved diversity. The basal unconformity of the Aseri stage is placed at 463.4 Ma in our time scale, and does correspond to a preserved diversity minimum. However, a declining trend in biodiversity is apparent long before the unconformity, so the hiatus itself can not be the only explanation. Similarly, the widespread unconformities from the Oandu to the Nabala stages are placed within a longer declining trend in biodiversity.

Large unconformities are less well developed in the Norwegian successions. None of the biodiversity minima in the Norwegian curve are easily correlated with unconformities, with the possible exception of the partial unconformity of the uppermost Solvang formation in the Oslo-Asker district. However, the biodiversity minimum at 450 Ma occurs slightly later, and again the phase of low biodiversity is also of far too long duration to be explained by this hiatus alone.

To conclude, there is no strong support for correlation between the presence of unconformities and low preserved biodiversity. This must be due to relatively intensive sampling in the area, which "rescues" the curve even at times of little preserved rock volume. In Sweden, the successions of the Siljan district are probably relatively continuous. Robustness to random reduction of the data set was formally tested by Hammer (in press), supporting this conclusion.

Spectral analysis of the diversity curve for the Ordovician of Norway, with the first and last time slice removed, gives an extremely strong and statistically significant peak for a frequency of about 0.075 periods per million years, corresponding to a period of 13.5 million years (Fig. 3). The significance test given by Press et al. (1992) reports a probability of $p < 0.001$ for this periodicity to result from random data. The power of the peak is 9.83, compared with a maximum peak power of 3.57 in the randomly reshuffled signal. The broadness of the peak is partly due to the increase in amplitude through the Ordovician. Using a sinusoid multiplied with a linearly increasing ramp as a model, the expected spectrum will be the sinusoidal spectral impulse convolved with the spectrum of the ramp, producing some spectral smearing (e.g. Proakis & Manolakis 1992). Autocorrelation (Fig. 4) similarly gives a clear peak for a lag time of

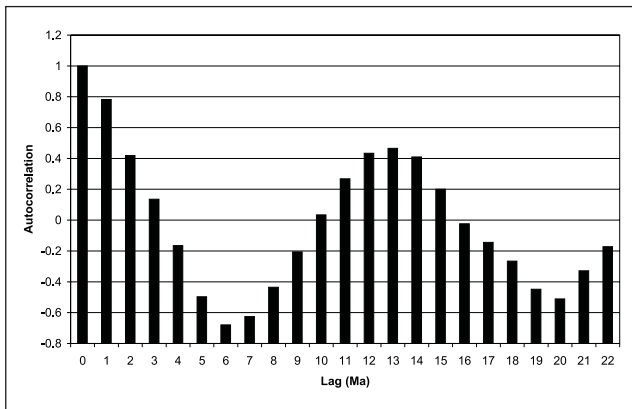


Fig. 4. Autocorrelogram of the Ordovician diversity curve for Norway. A high correlation coefficient is observed for a lag time of 13 million years, implying periodicity.

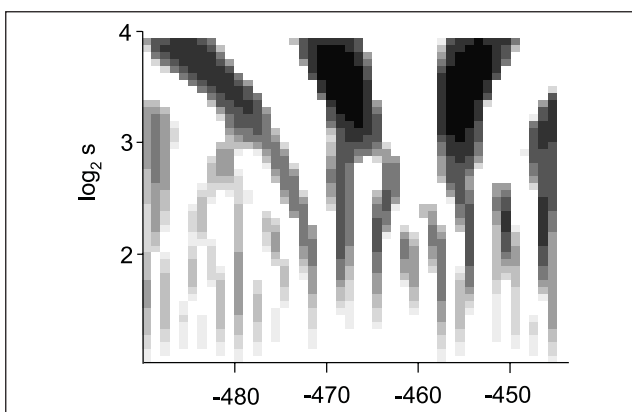


Fig. 5. Continuous wavelet scalogram of the Ordovician diversity curve for Norway, based on the Morlet wavelet basis. The vertical axis is in units of the logarithm (base 2) of the scale at which the time series is observed. For example, at $\log_2(s)=3$, the signal is observed at a scale corresponding to $s=2^3=8$ million years. Signal strength (correlation with the wavelets) is shown in a grayscale. Strong periodicity is visible at a scale of around 12 million years.

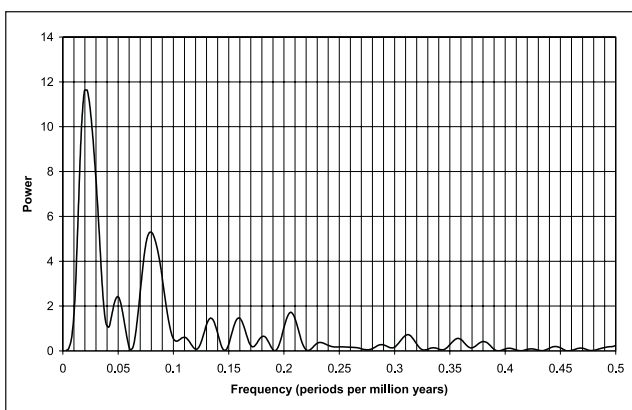


Fig. 6. Spectral analysis of the Ordovician diversity curve for Sweden, showing a weak spectral peak for a period of 12.5 million years (0.080 periods per million years). The stronger peak at 0.02 periods per million years corresponds to a single cycle of 50 million years and does not imply periodicity. $p=0.05$ significance level is at a power of 7.5, $p=0.01$ at 9.1.

13 million years. The wavelet analysis (Fig. 5) again shows four main cycles at a scale of $\log_2 s=3.6$, corresponding to a periodicity of approximately 12 million years.

The spectral analysis of the Swedish data shows a strong peak corresponding to a single cycle, which can not be taken to indicate periodicity. The next peak at a frequency of 0.08 periods per million years corresponds to a period of around 12.5 million years (Fig. 6), but the amplitude power of the peak (5.28) is reduced to about half of that of the 13.5 Ma cyclicity observed in Norway. The peak is not significant at a $p<0.05$ level using the white-noise floor test of Press et al. (1992), but stronger than the strongest peak in the randomly reshuffled sequence (power 3.51). The autocorrelogram shows only a broad and low peak for a lag time of 10–12 million years (Fig. 7). Wavelet analysis (Fig. 8) clearly indicates four main cycles at a scale of $\log_2 s=3.6$, corresponding to a periodicity of around 12 million years. Considering the uncertainties in estimating the period from the relatively wide spectral peaks, and probable errors in the time scale, the slightly shorter period in Sweden compared with Norway should not be over-interpreted.

Discussion

A periodicity of 12–14 million years has been demonstrated for biodiversity changes in the Ordovician of Norway, whereas a periodicity of 12–13 million years is possible for Sweden. The statistical significance is high for the Norwegian periodicity, but only three or four cycles are observed in the time interval studied. The estimated period (in units of inverse time) is of course also sensitive to errors in estimates of absolute ages (Muller & MacDonald 2000).

Although the main purpose of this paper is simply to present the statistical evidence for periodicity in taxonomic richness in the Ordovician of Scandinavia, it should be mentioned that the cycles partly correspond to second or third order transgressive cycles in the area, with high diversity at low sea level. For Sweden, we may compare the diversity curve with the sequence stratigraphic analysis by Dronov & Holmer (1999) and the sea-level curve for the Arenig given by Nielsen (1992). The diversity minimum at 476–473 Ma (middle Billingen stage) corresponds to high sea level. The diversity peak from 470–466 Ma (Volkhov-Kunda) corresponds to low sea level according to Nielsen (1992), while Dronov & Holmer (1999) indicate a more complicated development under generally deeper conditions. Correlation between diversity and sea level is less straightforward in the Upper Ordovician. For Norway, detailed sea level curves are not available, but the curve

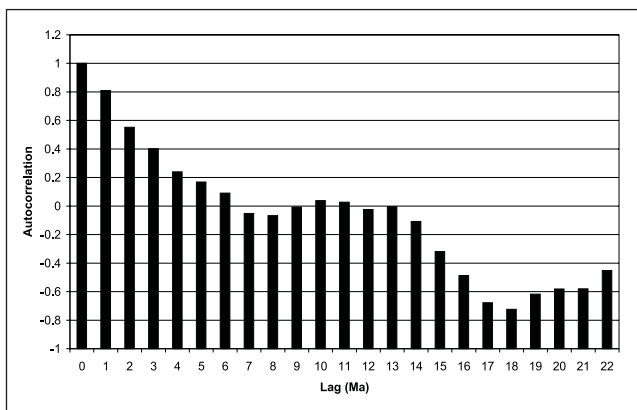


Fig. 7. Autocorrelogram of the Ordovician diversity curve for Sweden. A small peak in the correlation coefficient is observed for a lag time of 10-12 million years, implying weak periodicity.

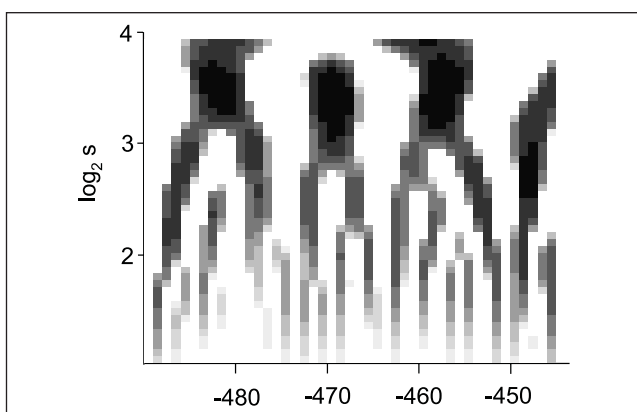


Fig. 8. Continuous wavelet scalogram of the Ordovician diversity curve for Sweden, based on the Morlet wavelet basis. Periodicity is visible at a scale of around 12 million years.

for the Arenig by Nielsen (1992) and the general description of Bruton et al. (1985) indicate a clear negative correlation between biodiversity and sea level. The diversity curve in the Hunneberg stage (484-477 Ma) corresponds well with the sea level curve of Nielsen (1992), with higher diversity during low sea level. The Billingen stage (477-472 Ma) shows low diversity at high sea level. The shallowing of the Volkhov and Kunda stages (472-463 Ma) corresponds to a diversity peak, while the succeeding Llanvirn transgression (Bruton et al. 1985) corresponds to a diversity minimum. The Caradoc regression and the transgression at the Caradoc-Ashgill boundary (Bruton et al. 1985) again correspond to respectively a maximum and minimum in the diversity curve.

The diversity curves may therefore to some extent be controlled by sea level through both ecological (Gray et al. 1997) and taphonomic (Koch 1998) processes. For example, the second (late Arenig) peak in Norway coincides with the Huk Formation (Owen et al. 1990), which is a unit consisting of bedded and nodular car-

bonates facilitating the preservation of shelly fossils. According to Nielsen (1992) and Bruton et al. (1985) the Huk Formation was deposited under relatively shallow conditions. The larger amplitude of the cycle in Norway than in Sweden may be connected with the different positions along the depth gradient, at least in the Lower and Middle Ordovician, although the relationship is contrary to an expectation that deeper-water communities would be less sensitive to sea-level change. One possibility is that the cratonic (Swedish) localities were always shallower than a certain threshold, keeping them within some narrow diversity range, while the offshore localities oscillated between deep-water, low-diversity conditions and shallow-water, higher diversity conditions, producing larger amplitude in the diversity fluctuations. The increased diversity at low sea level is in conflict with the idea of decreased diversity as a consequence of smaller areas of continental shelf at low sea level (Wyatt 1993, Rosenzweig 1996). At least at a local to regional (alpha diversity) level, such a species-area relationship can be hypothesised to be masked by effects such as increased fragmentation of habitat at low sea level, increasing diversity in relatively shallow localities (Gray et al. 1997), and low preservation potential in deeper water (Koch 1998). Also, the high sampled diversity at low sea level is in conflict with the study of Smith (2001), who observed low diversities at low sea level, presumably because of smaller sedimentary rock outcrop area. Measurement of rock outcrop area has not been carried out as part of this study.

If preserved faunal diversity in the Ordovician of Baltica was controlled by sea level, it implies a strong periodicity in the latter, prompting the question of possible mechanisms. Putative mechanisms for second and third order transgressive cycles such as changes in spreading rates at midocean ridges (Hays & Pitman 1973) and True Polar Wander (Mound & Mitrovica 1998) have not been shown to be inherently periodic.

Volcanic activity can probably be ruled out as a source of periodicity in this case. The enormous eruptions in the Middle Ordovician, connected with the closing of the Iapetus ocean, seem to have had minimal effect on the biotas (Huff et al. 1992). Indeed, the thickest bentonite bed in Baltoscandia, known as the Kinnekulle K-bentonite or the Big Bentonite (Bergström et al. 1995), occurs at the base of the Keila stage. This is placed at 455 Ma in the time scale used here, shortly before the strong Caradoc peak in the diversity curves of Figure 2. A negative effect of these eruptions on taxonomic richness can therefore not be detected.

The processes responsible for cyclicity in marine faunal diversity in general, and the 12- to 14-million years cycle in the Ordovician of Norway in particular, remain so far unexplained.

Acknowledgements. - This work was supported by the Norwegian Research Council, and is a contribution to IGCP410 'The great Ordovician Biodiversification Event'. I am grateful to Alan Owen and Svend Stouge for their useful comments on the manuscript.

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