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Using abundance data to assess the relative role of sampling biases and evolutionary radiations in Upper Muschelkalk ammonoids

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The Middle Triassic ammonoid genus *Ceratites* diversified spectacularly within the Germanic Muschelkalk Basin during the Anisian/Ladian (244–232 Mya). Previous studies have interpreted this diversification as a sequence of rapid, endemic radiations from a few immigrant taxa. Here we investigate the possibility that geological and sampling biases, rather than ecological and evolutionary processes, are responsible for this pattern. A new specimen-based dataset of *Ceratites* species-richness and abundance was assembled. This dataset was combined with 1:200 000 geological maps in a geodatabase to facilitate geospatial analyses. One set of analyses compared species richness per geological map with the number of occurrences and localities per map. Per-map change in the amount of rock available to sample for fossils was also included as a variable. Of these three variables, number of occurrences is the most strongly correlated with richness. Variation in the amount of rock is not a strong determinant of species-richness. However, rarefaction of basin-wide species/abundance data demonstrates that differences in species-richness through time are not attributable to sample size differences. The average percent similarity among sites remained close to 50% throughout the Upper Muschelkalk. The rank abundance distribution (RAD) of species from the first interval of the Upper Muschelkalk is consistent with colonization of a disturbed environment, while the other two intervals have RADs consistent with more stable ecosystems. These results indicate that genuine ecological and evolutionary events are partly responsible for the observed differences in richness and abundance. Although changes in the RADs through time support changes in the ammonoid assemblage structure, the processes underlying increasing richness and change in RADs cannot be explained by increasing geographic distinctiveness or isolation among the ammonoid assemblages present at different localities.

Key words: Ammonoidea, *Ceratites*, biodiversity, rank abundance, palaeoecology, Muschelkalk, Triassic.

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Introduction

Instances of rapid diversification within restricted geographic areas represent "natural experiments" for the study of the mechanisms responsible for generating and controlling richness and abundance patterns (Schluter 2000). The cichlid flocks of the African Rift Lakes (Meyer 1993) and the radiation of *Geospiza* (Darwin's finches) on the Galapagos Islands are two exemplars of geographically restricted radiations among living taxa. McCune (1990, 1996) provided convincing evidence that such events can be detected in the fossil record as far back as the Triassic among *Semionotus* fish in rift-basins.

The evolutionary history of *Ceratites* de Haan, 1825, the iconic ammonoid of the Triassic, represents another geographically restricted radiation in the fossil record. *Ceratites* is a species-rich genus confined to the epicontinental seas in and adjacent to the Germanic Basin during the Anisian and Ladinian (Tozer 1981; Page 1996). The stratigraphy and timing of ammonoid immigrations into the Muschelkalk Basin are sumarized in Fig. 1.

The evolution of *Ceratites* within the Germanic Basin during the Upper Muschelkalk has been described in a number of previous papers (Wenger 1957; Hagdorn 1991; Ulrichs and Mundlos 1985, 1990; Klug et al. 2005). *Ceratites* first appeared in the Muschelkalk Basin after a basin-wide interval of

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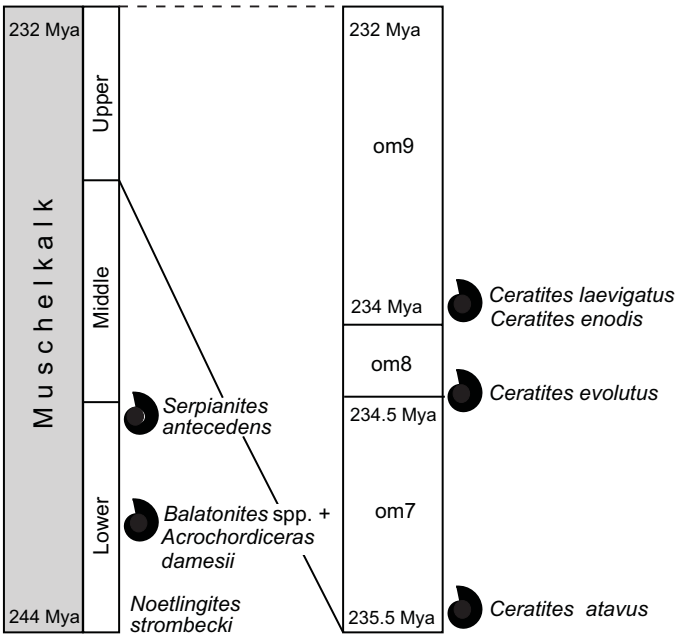


Fig. 1. Chart of stratigraphic interval names and durations for the Muschelkalk of the Germanic Basin with ammonoid immigration events marked (simplified from Klug et al. 2005: fig. 1).

hypersalinity marked by extensive evaporitic deposits during the Middle Muschelkalk (Hagdorn 1991; Klug et al. 2005). The genus diversified rapidly over ~3.5 Myr within the restricted Muschelkalk Basin and Klug et al. (2005) have presented detailed morphological evidence for the relative roles of immigration from Tethys and endemic evolution of the genus within the basin, supporting earlier work by Ulrichs and Mundlos (1985) on the entry of the ammonoid lineages into the German Muschelkalk Basin via "gateways" from the Tethyan Ocean and their subsequent raditiation. Other major groups, including crinoids and nautiloids immigrated into the basin at various points, but did not undergo the same degree of radiation as the ammonoids (Ulrichs and Mundlos 1985). This is despite the faunal exchange of these two groups with Tethys being apparently mediated by the same patterns of sea-level rise and fall (Klug et al. 2005: fig. 1).

If the mechanism(s) responsible for ceratite radiation are to be more fully understood, information about the spatial distribution of taxa is also required. If spatially heterogeneous processes, such as habitat specialization or geographical isolation, dominated in the speciation mechanisms that led to the diversification of *Ceratites*, this could be detected by changes in the degree of similarity among locations within the basin through time. Increased geographic isolation would be reflected by significant decreases in similarity among sites through time. Bayer and McGhee (1985) discussed two end-member modes of diversification in epicontinental seas based on well-established speciation mechanisms. Speciation can either be driven by regression events, with physically separated populations forming new species by allopatry/peripatry, or during transgression events, when a new range of habitats, appear and speciation proceeds by ecological specialisation. Yacobucci (1999) invoked these models to explain the radiation of acanthoceratid ammonites in the Western Interior Seaway, but came to no firm conclusion about the relationship between ammonite diversification and transgression/regression sequences.

Both Bayer and McGhee (1985) and Yacobucci (1999) relied heavily upon phylogenetic evidence to resolve the likely speciation mechanism(s), while treating the observed changes in species-richness as a real phenomenon. Ecologists regularly assess how species-richness is related to the number of individuals collected, the number of sites and the range of habitats sampled (Rosenzweig 1995; Hayek and Buzas 1997; Gaston and Blackburn 2000). Palaeobiologists have come to understand the problems of using unstandardized richness data and now routinely compensate for potentially misleading differences in sampling effort in palaeobiological studies (e.g., Alroy et al. 2001, 2008; Bush et al. 2004; Kowalewski et al. 2006).

Palaeontologists must also account for the possibility that changes in richness and abundance result from geologically-mediated biases (Raup 1972, 1976; Holland 2000; Peters and Foote 2001, 2002; Crampton et al. 2003; Smith 2007). The sequence stratigraphy of the Muschelkalk has been well-studied (Aigner 1985; Aigner and Bachmann 1992, 1993). Ulrichs and Mundlos (1990) established a strong connection between some parasequence boundaries and the evolution of *Ceratites*. Eustatic fluctuations may force genuine changes in the environment and faunal assemblage. However, Holland (1995, 1999, 2000) presented convincing evidence from simulation studies, that first and last occurrences of taxa may be strongly and systematically controlled by sequence-stratigraphic architecture. These models were derived from observations, such as those observed by Ulrichs and Mundlos (1990), of the clustering of first and last occurrences of taxa at sequence boundaries. The models were verified by subsequent field-based studies (e.g., Patzkowsky and Holland 1996). Our first objective is thus to thoroughly explore whether sampling and/or geological biases alone could account for the changes in species-richness through time among the Upper Muschelkalk ammonoid fauna before seeking biological explanations for the changes.

Even if the gross pattern of changes in species-richness through time can be explained by differences in sample size alone, this does not preclude the possibility that real changes in the *Ceratites* assemblage occurred within the Upper Muschelkalk. As the conditions of the Germanic Basin altered from the hypersaline conditions of the Middle Muschelkalk to the more normal marine conditions of the Upper Muschelkalk, a change from uneven assemblages associated with initial re-colonization to more even communities in the later part of the Muschelkalk is to be expected. Quantitative comparison of the RADs of species among the three intervals offer the tracking from disturbed to more stable communities occurred during the Upper Muschelkalk (Anderson et al. 1996; Magurran 2004; Hammer and Harper 2006). Basin-wide analyses can be combined with analyses of the similarity of taxa among differ-

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ent sites to search for marked differences in the distribution of taxa across the Muschelkalk Basin through time. Decreasing similarity among localities could be associated either with spatially-restricted diversification or the restriction of immigrant taxa to certain areas.

Through analysis of richness and abundance data from localities at multiple spatial scales, a more nuanced understanding of the relative roles of sampling bias and ecological and evolutionary processes in the evolution of *Ceratites* in the Upper Muschelkalk can be gained.

Institutional abbreviations.—BGR, Bundesanstalt für Geowissenschaften und Rohstoffe, Spandau, Germany; GPMM, Geologisch-Paläontologisches Museum Münster, Germany; MfN, Museum für Naturkunde, Berlin, Germany; MHI, Muschelkalk Museum, Ingelfingen, Germany.

Other abbreviations.—HST, highstand tract; RAD, rank abundance distribution; TST, transgressive systems tract.

Material and methods

Sampling of individual ammonoid specimens.—The taxonomic name, geographic and stratigraphic information were recorded for a comprehensive set of ammonoid specimens in collections held at the MfN, BGR, MHI, and GPPM, comprising over 3000 individuals. Ulrichs (2006) recently revised the taxonomy of *Ceratites*, abandoning the older subgeneric classifications. Older taxonomic names were updated to provide a uniform taxonomic classification of specimens. Museum collections, were used for two reasons. Firstly, museum collections have been shown to be consistently better at sampling rare taxa than field collections (Guralnick and van Cleve 2005; Grytnes and Romdal 2008; Harnik 2009). Secondly, by working with original specimens it was possible to check and revise taxonomy in a uniform fashion. McGowan (2009) also presented a cladistic study of the taxa included in this paper and all were supported by autoapomorphies. This removes the possibility that any of the taxa in our samples could be placed as ancestors in anagenetic lineages, but does not completely rule out the influence of form taxonomy upon species designations.

Georeferencing of specimens.—Georeferencing of the material, the process of converting text-based locality descriptions into geographic co-ordinates, was performed using BioGeomancer (Guralnick et al. 2007). BioGeomancer returns present-day geographic co-ordinates for named localities. The precision of BioGeomancer varies, but is usually accurate to within 10 km, a level of accuracy considered acceptable in many modern biodiversity studies at similar spatial scales (e.g., Gibbons et al. 1993). Even when data are recorded with greater precision by individual recorders these data then tend to be aggregated to 10 km resolution for analytical work. Global analyses in palaeobiology (e.g., Alroy et al. 2008) will often include data with only about 100 km precision. Locality information was validated, wherever possible, using additional information associated with specimens held by BGR. BGR fossils are associated with a particular geological map area they were collected from. In a few cases, noted in the supplementary data table (SOM, Supplementary Online Material at http://app.pan.pl/SOM/app58-McGowan_Kiessling_SOM.pdf), this became the primary means of georeferencing where the locality information on the label was vague. Specimens that could not be georeferenced were excluded from further analyses.

Stratigraphic subdivision of specimen occurrences.—While fine stratigraphic control based on ammonoid zonation and marker beds is possible within the Muschelkalk (Hagdorn 1991, 2004; Klug et al. 2005), many museum specimens lack precise stratigraphic information. Therefore, the samples were stratigraphically pooled based on well-recognized broad divisions of the Upper Muschelkalk: om7, om8, and om9 (see Fig. 1). The duration of these divisions is estimated at about 1 Myr for om7, 0.5 Myr for om8, and 2 Myr for om9 (Menning et al. 2005). Specimens were assigned to the appropriate stratigraphic interval where possible and those that could not be assigned to a stratigraphic interval were removed from the database, leaving 1033 specimens distributed among the three stratigraphic intervals.

The sequence stratigraphy of the Muschelkalk has been well-studied (Aigner 1985; Aigner and Bachmann 1992, 1993) and cycles are resolved to a relatively fine-scale. However, given the broad division of specimens into the three intervals outlined above, only the larger-scale patterns can be discussed in this study. The Upper Muschelkalk experienced an overall sea-level rise until its end. Both om7 and om8 are considered to be part of the transgressive systems tract (TST), with om9 being designated the highstand tract (HST).

Geoinformation Systems processing of data.—The resulting occurrence files for each interval were plotted in ArcInfo using the latitude and longitude information derived from the georeferencing work. Fig. 2 shows the localities plotted for each interval on map of modern Germany.

The complete set of rasterized BGR 1:200 000 general geological maps (downloadable from http://www.bgr.bund.de/EN/Themen/Sammlungen-Grundlagen/GG_geol_Info/Karten/Deutschland/GUEK200/guek200_inhalt_en.html) were imported into ArcInfo and the map corners registered to the appropriate co-ordinates. Most of these 1:200 000 maps cover approximately equal areas and were used as a sampling grid (see Smith and McGowan 2007). For each stratigraphic interval, the number of occurrences, number of localities and species-richness was compiled for each map. The proportion of grid squares on each map with some Muschelkalk outcrop was calculated by overlaying a 9 × 9 grid on each map, using the grid option in the "View" window of ArcInfo, resulting in rectangular cells about covering 30 km of latitude and 40 km of longitude. Each grid square was checked for the presence of Muschelkalk rock (hereafter, Muschelkalk outcrop occur-

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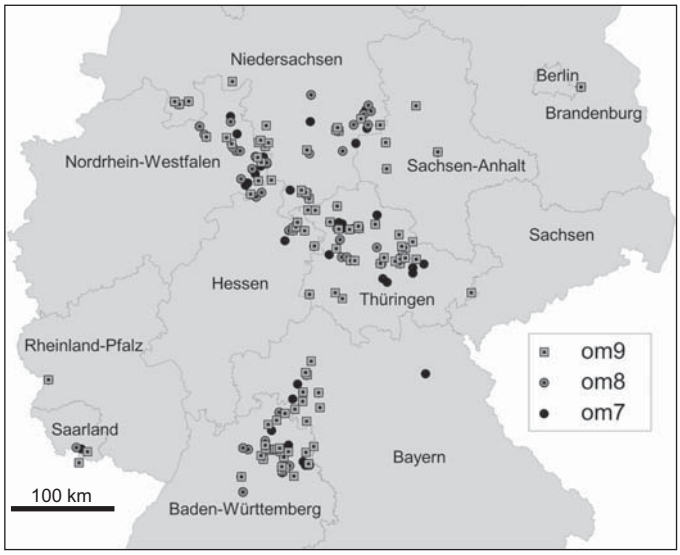


Fig. 2. Distribution of Muschelkalk ammonoid localities used in this study plotted on a map of modern Germany. The overall geographic spread of localities does not change greatly over time.

rence). Hereafter, the data for each map will be referred to as the "per-map" dataset.

Correlation analyses between richness and sampling effort variables.—To meet the assumptions of a normal distribution required for Pearson Correlation and least-squares regression modelling, data were $\log_{10}$ transformed prior to correlation analysis except for Muschelkalk outcrop occurrence. Pairwise correlations between richness per map and per map sampling effort variables (occurrences, localities and Muschelkalk outcrop occurrence) were calculated. To explore the possibility of non-independence among the per-map sampling effort variables, partial correlation analysis was also performed.

Calculation of similarity between localities.—Spatial variation in the species composition of *Ceratites* assemblages was assessed to similarity among the three intervals. Occurrence data were aggregated into 1 × 1 degree bins and the percent similarity metric is used to measure similarity among bins for each time interval. Percent similarity has the desirable property of being relatively insensitive to differences in sample size (Gauch 1982).

Analysis of relative RADs.—RAD distributions were constructed for each interval, based on all occurrences of all ammonoid specimens from that interval. Peters and Bork (1999) and Lockwood and Chastant (2006) have set a precedent for the investigation and interpretation of the fit of model distributions to palaeontological data has precedents that are relevant at larger spatio-temporal scales than usually applied in ecology, where the techniques were developed. The spatio-temporal extent of the work of Peters and Bork (1999) in the Ordovician is of the same order as the Muschelkalk Basin. Lockwood and Chastant (2006) showed that while the absolute values of biodiversity metrics tended to decrease, the shape of the RADs tended to be unaltered and it

Table 1. Information on richness, number of occurrences and number of locations per map for each interval. Map numbers refer to BGR designations.

Interval om7			
Map	Richness	Occurrences	Locations
3910	3	4	3
3918	3	4	3
3926	9	56	16
3942	3	8	1
4710	0	0	0
4718	10	92	28
4726	8	21	11
5518	6	8	2
5526	10	28	12
5534	2	3	3
6302	0	0	0
6318	1	2	2
6326	1	2	2
7102	1	1	1
7118	10	42	10
7126	10	57	5
Interval om8			
Map	Richness	Occurrences	Locations
3910	2	3	3
3918	1	2	2
3926	5	17	10
3942	4	7	1
4710	2	4	1
4718	9	51	20
4726	10	31	13
5518	0	0	0
5526	8	29	18
5534	0	0	0
6302	1	1	1
6318	2	2	2
6326	1	1	1
7102	1	1	1
7118	9	138	14
7126	4	8	2
Interval om9			
Map	Richness	Occurrences	Locations
3910	2	2	2
3918	1	2	2
3926	5	13	5
3942	2	2	1
4710	1	1	1
4718	11	73	33
4726	12	28	13
5518	0	0	0
5526	10	27	17
5534	2	2	3
6302	1	1	1
6318	6	14	4
6326	14	59	5
7102	4	6	3
7118	19	164	19
7126	5	17	5

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is the shape of the distribution that is the critical aspect of such analyses.

To allow direct comparison among the three intervals with uneven numbers of individuals, the occurrence data were also transformed into proportional data. Preliminary investigations in PAST found that the transformation made little difference to our model fits, which allowed us to use the Vegan package in R. The RAD distribution for each interval was then compared to five widely used hypothetical distributions available in Vegan package (Oksanen et al. 2011) in R (R Development Core Team 2011) using the radfit command (broken-stick [null in radfit], geometric, log-series, log-normal Zipf and Zipf-Mandelbrot).

Results

Standing richness and speciation rates for *Ceratites*.—Based on the occurrences of species regarded as valid by Ulrichs (2006), species-richness increased during the course of the Upper Muschelkalk, with a major increase in richness during the terminal om9 interval. Speciation rates are highest during the om8 interval (24 species per Myr) and lowest during the om9 (7.5 species per Myr). One difficulty with calculating speciation rates is that the first appearances of some species in the Germanic Basin are possibly attributable to immigration.

Relationships among sampling variables and species-richness.—Table 1 lists the number of occurrences and localities per map, the proportion of grid squares on each map with Muschelkalk at outcrop, and associated species richness. The longest interval, om9, has the highest number of occurrences and localities, while om8 has the lowest number of both, although not much lower than om7. The number of maps with Muschelkalk ammonoid occurrences remains almost constant at 14 maps out of the 58 maps for the om7 interval and then 15 maps for remaining two intervals, although which particular maps contained ammonoid-bearing localities varies among the three intervals. Coupled with the pattern of occurrences in Fig. 2, this demonstrates that the overall area that rocks and occurrences are distributed over through time is not subject to major fluctuations.

Correlations between richness and number of occurrences/localities per map are positive and highly significant for all three intervals (Figs. 3 and 4).

Variation in these two sampling effort measures explains 70–90% of the variation in per-map richness. Correlations between Muschelkalk outcrop occurrences, number of localities and richness were also calculated. The correlation coefficients are lower than those for the relationship between richness and occurrences and richness and number of localities, in the range of 0.5–0.7, but these lower correlations explain much less of the variance in richness than the number of occurrences or number of localities per map (25–50% less).

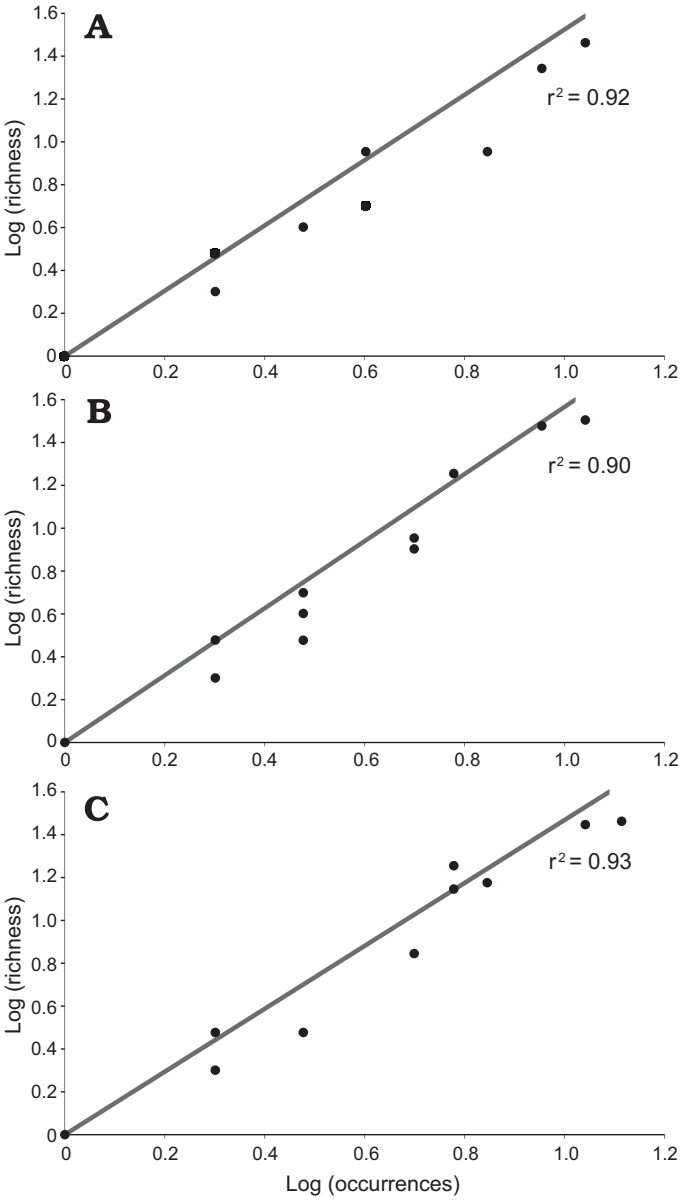


Fig. 3. Correlations between richness per map and number of occurrences. **A**. om7 interval. **B**. om8 interval. **C**. om9 interval.

In all three intervals the best predictor of richness per map is the number of occurrences. The largest difference between predictors is for om9, with number of occurrences explaining 13% more of the variance than number of localities.

Partial correlations, which account for non-independence among variables, were calculated with richness as the dependent variable and occurrences, localities and Muschelkalk outcrop occurrences as explanatory variables (Table 2). The partial correlation values between richness and occurrences are positive and highly significant. For all three intervals, none of the partial correlations between richness and localities or richness and Muschelkalk outcrop occurrences are significant, which implies that both the number of localities and percentage of grid squares with outcrop are not independent variables.

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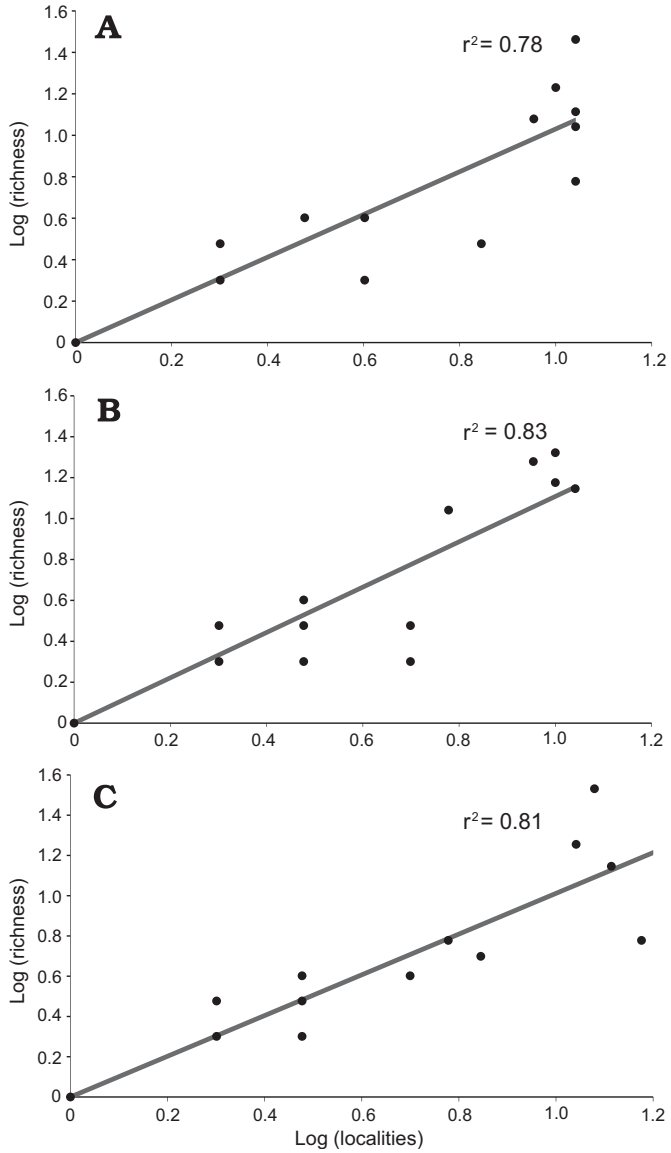


Fig. 4. Correlations between richness per map and number of localities. **A**. om7 interval. **B**. om8 interval. **C**. om9 interval. The gap in the distribution of points for the om8 interval highlights the discontinuity between a group of maps with few taxa at a few localities and other maps with a large number of localities and high richness.

Rarefaction.—Although the correlation and partial correlation analyses indicates that sampling effort is exerting a strong influence on richness estimates at the per map scale, this does not exclude the possibility that the basin-wide differences in richness among the three stratigraphic intervals are real. Rarefaction curves were generated for each interval based on the number of occurrences (Fig. 5). The hypothesis that differences in sample size are responsible for the extra richness of om9 can be rejected at a sample size as low as 50 occurrences, where the 95% confidence intervals cease to overlap. However, the significantly higher richness of om8 relative to om7 only becomes apparent at around 250 occurrences.

Similarity among sites through time.—The network of lines on Fig. 6 indicates the similarity among each group of sites, which ranges from relatively low values for some of the more isolated sites, such as the taxa from the Saarland in the far south-west (Fig. 6). The average percent similarity for each interval is around 0.5.

The central area of the map is dominated by relatively high similarity among sites, even relatively far from the proposed "gateways" that lie to the SE and SW of the Basin. Following Miller et al. (2009) correlation analyses of plots of geographic distance between sites found no significant relationship between these two variables in the first two intervals, followed by a significant relationship during the om9 interval. A further analysis that compared the mean similarity between the node at the centre of the basin (51°N, 10°E) with the mean similarity of all other nodes also found evidence that the circa 10% greater similarity of sites linked to the centre of the basin was significantly higher than the values for more peripheral areas (Table 3). Examination of the mean similarity between the centre and periphery of the basin through time allows some insight into the temporal evolution of this pattern. Much of the signal in the combined data set comes from om7 and om8 and then in om9 the pattern reverses to such an extent as to render the differences not statistically singificant.

Relative rank abundance distributions through time.—Table 4 lists Akaike Information Criterion (AIC) scores for each interval and the five theoretical distributions invoked with the radfit command in the Vegan Package are listed in Table 3. The best fit to the om7 RAD distribution is the geometric series. Support for the Zipf-Mandelbrot power-law model is also high. For interval om8 the best fit is the log-normal model with the Zipf model having some support. For the om9 data the Zipf-Mandelbrot model is the best fit but the log-normal model is a viable alternative.

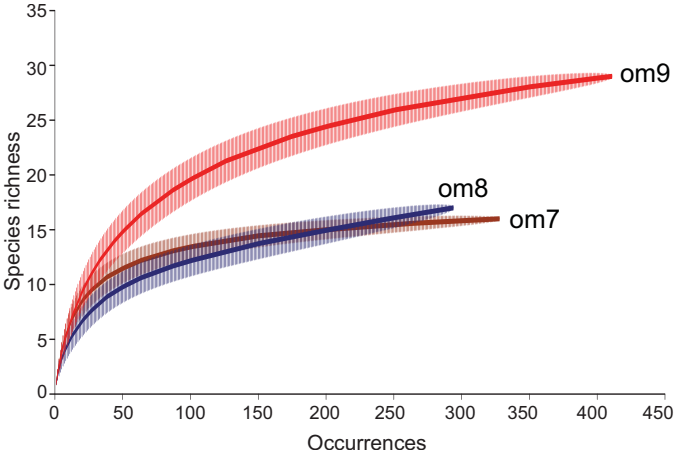


Fig. 5. Rarefaction curves for each interval, based on number of occurrences. The confidence envelope of the species richness for om9 departs significantly from those of om7 and om8 above 50 occurrences, but the significantly higher species-richness of om8 only becomes apparent at sample sizes of around 250 specimens, indicating that a few, rare taxa are boosting richness in the om8 interval.

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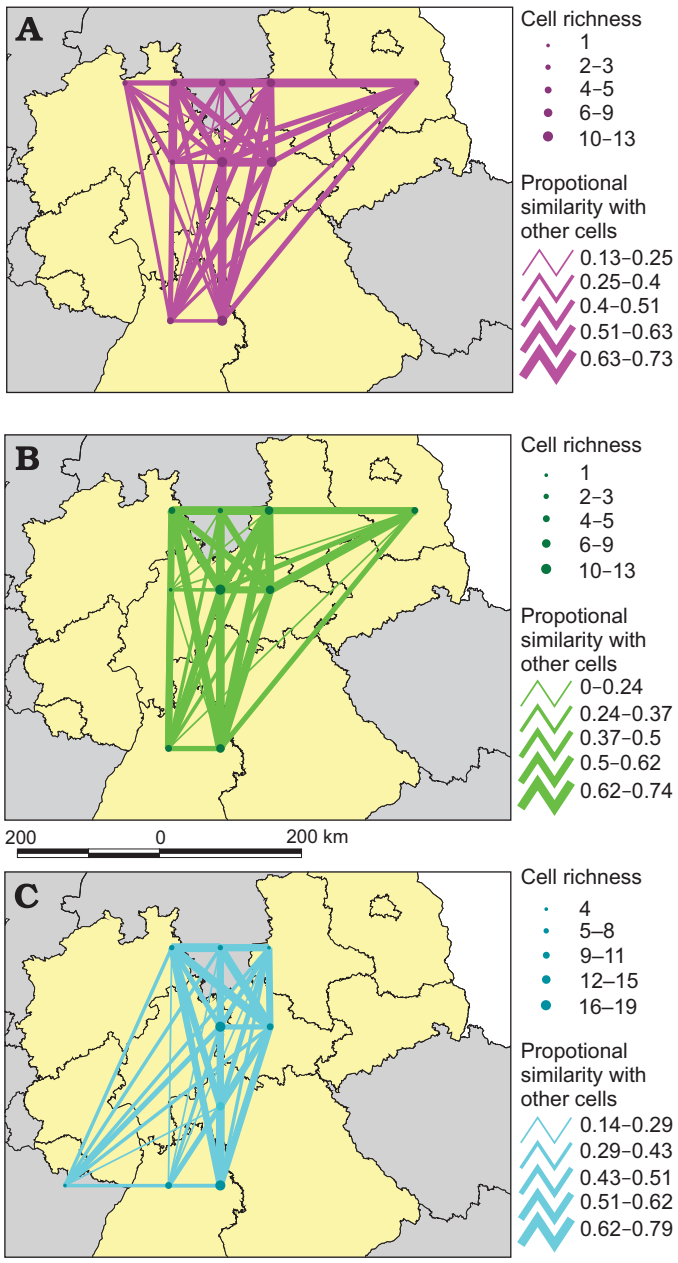


Fig. 6. Percent similarity among bins averaged to 1 degree bins. **A**. om7 interval. **B**. om8 interval. **C**. om9 interval. The thicker the line, the greater the similarity between the two cells connected by the line.

Discussion

The results described above indicate that the change in species-richness through time in the Germanic Basin is a real phenomenon and the additional spatial information and abundance data permits new, quantitative insights into the processes that are responsible for the increase in richness through time. The accumulation of species-richness calculated for *Ceratites* is an order of magnitude lower than examples of species-flocks of fishes (Greenwood 1981; McCune 1990, 1996) and Cretaceous ammonites (Yacobucci 1999), but the radiation of *Ceratites* remains an important case of a radiation within a restricted area in the fossil record.

Per-map richness is controlled by sampling effort.—The number of specimens collected per-map is a consistently good predictor of richness and the partial correlation analysis indicates that this relationship is not confounded by non-independence between occurrences and other relevant variables. Although the number of localities per map also has a strong, positive correlation with richness, the partial correlation analysis reveals that localities are not independent of the number of occurrences. Localities and occurrences have an inherent positive correlation; to add a new locality requires at least one new occurrence. Muschelkalk outcrop occurrences per map do not predict as much variability as the number of occurrences or localities when used as an independent variable. Muschelkalk outcrop occurrences are also not independent of occurrences. The source of the non-independence is not clear here, as it is perfectly possible to have large areas of outcrop barren of fossils and small areas that are very fossiliferous. Whatever the underlying mechanism, the hypothesis that geological outcrop patterns are exerting an important control upon sampling patterns on a per map basis is not supported for the Upper Muschelkalk ceratites.

Table 2. Partial correlations between richness and other variables for each interval (** = p-value between 0.05 and 0.01, *** = p-value < 0.01).

	Occurrences	Localities	Proportions
om7	0.85***	-0.21	0.45
om8	0.7**	0.43	-0.37
om9	0.86***	0.18	-0.13

Table 3. Non-parametric comparison of average similarity values for nodes linked to the central node in the basin (51°N, 10°E) and values for linkage between other peripheral nodes. Comparisons are given for each interval and an overall value.

	om7	om8	om9	Combined
Periphery average similarity	0.272	0.286	0.403	0.322
Centroid average similarity	0.431	0.424	0.361	0.405
p-value	0.01	0.07	0.362	0.028

Table 4. AIC values of five models using the radfit command in the Vegan package in R. The best model is in bold and the AIC difference to the next best fit is given in brackets for the second best model fit. Burnham and Anderson (2002) estimated that an increase in AIC of less than 2 above the best model indicates that the alternative model should be given serious consideration, values of between 3 and 7 indicate considerably less support for those models and values over 10 make alternative models implausible.

	om7	om8	om9
Null (broken-stick)	84.24	276.07	204.68
Pre-emption (geometric)	**73.37**	205.69	100.68
Log-normal	88.55	**128.23**	80.15 (2)
Zipf	119.21	132.97 (3)	85.65
Zipf-Madelbrot	77.30 (4)	134.49	**78.78**

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Rarefaction indicates that basin-wide increase in richness through time is not a sampling artefact.—Although the results above indicate that a sample-size bias is responsible for variation of richness per map, rarefaction of the basin-wide samples from each stratigraphic interval indicates that the differences in species-richness among the three intervals is not a simple artefact of differences in sample size alone. The contrast between om9 and the other two intervals is striking but further study could reverse the relative richness values for om7 and om8. Throughout the basin, there is no variation in the Muschelkalk outcrop occurrence rate through time, so the role of rock availability can be rejected again.

By combining the results of the rarefaction and correlation analyses, it is possible to build up a more nuanced understanding of the relationship between sample size and species-richness. At the basin-wide scale, there is strong support that the increase in ceratite diversity through time is real. While the higher richness of om9 is clear at a fairly small sample size (> 50 occurrences), the hypothesis that differences in richness between om7 and om8 can only be rejected with a much larger sample size (> 250 occurrences). This distribution leads to the conclusion that it is the sampling of rare taxa from few localities on a few maps that reveals the higher diversity from om8. As the om7 and om8 rarefaction curves only differ significantly at high sample sizes, this further emphasizes the importance of these few occurrences in establishing the higher richness of the *Ceratites* during the om8 interval.

Another problem with a straightforward rejection of sample size as a factor is the difference in RAD distributions between om7 and om8. Rarefaction is sensitive to differences in the underlying abundance distribution, as it selects taxa at random (Wagner et al. 2006; Grytnes and Romdal 2008; Harnik 2009). However, we can be confident that the differences between om8 and om9 are not controlled by sample size, as they have similar abundance distributions. Bush et al. (2004) cautioned that changes in spatial organization of biodiversity might alter the trajectory of rarefaction curves but only interval om9 shows any signal of emergent spatial organization within the basin and we conclude that the most likely confounding factor is the shape of the RAD distributions, rather than any bias related to spatial organization.

Lack of geographic variation among *Ceratites* assemblages through time.—Among the sites aggregated to 1×1 degree bins, there is little evidence for substantial differences in the ammonoid assemblages across the basin through time. Taken in conjunction with the findings about the roles of other sampling variables, it is apparent that individual ceratite taxa are widely distributed across the basin, with no obvious control on richness at individual sites beyond that of sampling effort.

Any contention that individual ceratite species or groups of species are closely associated with particular areas and excluded from other areas is not supported by these findings. Previous studies have found associations between particular morphotypes and facies (Jacobs 1994; Wang and Westermann 1993), but no attempt is made here to provide comprehensive analysis of the link between facies and individual occurrences. The mixing of different morphotypes (smooth and compressed versus heavily ornamented and inflated) is often apparent within the lists of taxa from individual ceratite localities and the overall pattern of morphological change in the basin from small, ornamented forms during the om7 interval to the larger compressed forms during the om9 interval is suggestive of a phylogenetic rather than environmental control (Klug et al. 2005). Both Ulrichs and Mundlos (1985) and Klug et al. (2005) presented evidence for ontogentic changes being the major factor in the radiations, and the lack of evidence in this study for segregation of taxa in particular areas offers support that intrinsic, developmental factors may be the main source of morphological novelty and new taxa.

This study highlights the value of aggregating data at different scales. The correlation analyses would apparently support a hypothesis that the number of occurrences, which relates to sampling effort, is controlling richness, but at the basin-wide scale differences in sample size cannot alone explain differences in richness. It is likely that much of the variation among the assemblages results from individual outcrops representing random aggregations of species from the regional pool, as is the case for some modern groups, particularly those that are more mobile (e.g., distributions of birds and mammals; Gaston and Blackburn 2000). Ammonoids were probably more mobile during life than many of the other invertebrate groups co-occurring in the Muschelkalk and may also have drifted after death. (Ulrichs and Mundlos 1985). However, the role of post-mortem drift in the generation of ammonoid death assemblages is debatable. Ulrichs and Mundlos (1985) presented maps that plotted nautiloid taxa further towards the basin margins and the initial evidence for long-distance drift in modern *Nautilus* was the discovery of shells on beaches. Few ammonoid shells are found in intertidal deposits in the Muschelkalk. However, Kaim and Niedźwiedzki (1999) presented evidence for ammonoid shells drifting considerable distances to end up in the Lower Muschelkalk deposits of Poland.

A more general explanation for the differences in richness between the outcrop and basin scale from ecological perspective is that most of the richness is to be found at the among-collections level, which is only apparent at relatively large spatial scales. A future analysis of additive diversity partitioning could test this hypothesis in more detail, but would require a more spatially structured sampling scheme (e.g., Patzkowsky and Holland 2007).

Mac Nally et al. (2004) demonstrated that a finer sampling grid can reveal beta diversity patterns not detected at coarser resolution level but, based on these analyses, different ceratite species were not restricted to particular parts of the basin.

This leads on to a general unresolved issue is the exact nature of the discovery process of fossils. An important control on the amount of fossil material collected is likely to be the angle of dip. Near horizontal beds will offer potentially large areas to sample but will often not create a topography that allows

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much access to the rocks, except in quarries or valleys where the amount of each bed exposed will be limited. The other extreme are more steeply dipping beds, which may result in the exposure of large areas of individual bedding plane surfaces at a single site. The patterns of Muschelkalk ammonoid discovery demonstrate this phenomenon rather well. Many individual ceratite fossils have been recovered from quarries and river valleys (Hagdorn 1991, 2004). Two maps (BGR numbers 7118, 4718) have disproportionate numbers of occurrences that reflect both the influence of Hans Hagdorn's work at the MHI and the extensive network of quarries and river valleys in the Muschelkalk of Baden-Württemberg and Bayern. The topography of this region is of rounded hills created by river incision and some glacial influence and the Muschelkalk strata are relatively flat lying (Hagdorn 1991). A problem with attempting to make new field collections that include abundance data is that many of the quarries that ammonoids were collected from have either been closed or infilled, or previous collection work has removed many of the specimens. Future collection efforts should record as much geographic and stratigraphic data as possible, and would benefit from a pre-planned sampling programme (see Layou 2007 and Heim 2009 for exemplars).

The good fit of the om7 RAD data to the geometric distribution is consistent with the geological evidence of a genuine colonization event after the extirpation of ammonoids from the Germanic Basin during the Middle Muschelkalk. The geometric series is regarded as having an underlying biological cause: niche-pre-emption, which is associated with harsh or recently colonized environments where a few species will end up with the great proportion of the resources and is reflected in a highly uneven RAD distribution (Tokeshi 1999; Magurran 2004; Hammer and Harper 2006). As om8 and om9 are both best fitted by other models that reflect more stable ecosystems, the Muschelkalk ammonoid assemblages apparently became more stable after initial colonization during om7. While it is possible that the om7 RAD might represent a highly truncated log-normal distribution, due to the low sample size, it would then be difficult to explain why the om8 distribution is able to fill more octaves with even fewer samples. However, the large difference between the AIC of the geometric and log-normal models is powerful evidence against this argument. The Zipf-Mandelbrot model, which incorporates niche diversity and environmental predictability is the most credible alternative model for the om7 RAD. The log-normal model has an AIC value over 10 points higher than that for the Zipf-Mandelbrot, making it a poor model for the om7 data.

Two possible explanations exist for assemblages with log-normal distributions. The statistical explanation is that when a large number of factors determine the amount, in this case abundance, of a variable then the variable will be normally distributed due to the central limit theorem (May 1975). Sugihara (1980) argued that the species/abundance distributions of many assemblages across a range of taxa fit the log-normal distribution too well for the statistical explanation to be valid. Sugihara (1980) proposed that the log-normal distribution reflects splitting of niches into uneven fractions as new taxa join the community. Whether the log-normal is the result of sampling biases or biological processes, the log-normal is typical of speciose assemblages in stable, resource rich areas where large differences in local habitat exist. The RAD distributions record a shift from disturbed to more stable ecosystems within the Germanic Basin during the Upper Muschelkalk.

Occurrence and richness of *Ceratites* relative to Muschelkalk sequence stratigraphic architecture.—The relationship between sequence stratigraphic architecture and the evolution of *Ceratites* in the Germanic Basin has been remarked upon before (Ulrichs and Mundlos 1990; Aigner and Bachmann 1993). As the geographic extent of localities is similar among all three intervals, appealing to species-area mechanisms relationships related to increased flooding of the Basin, does not appear to offer a valid mechanism for generating increased diversity (Rosenzweig 1995). A rock-area effect is also unlikely, given the constant number of map sheets per interval with Muschelkalk outcrop and the results of the correlation analysis between Muschelkalk outcrop occurrence and richness.

The hypotheses that regression played an important role in *Ceratites* speciation is not supported by the results presented above. The om7 interval has the lowest species-richness, although an intermediate speciation rate. The calculated diversity per unit time, and the distribution of richness versus occurrences per map for om8, all lend some support to a burst of speciation toward the top of the TST, as the *Cycloides* Bank that marks the border between the om8 and om9 intervals is also the maximum flooding surface of the Upper Muschelkalk (Aigner and Bachmann 1992, 1993).

Analysis of assemblages of Valangian–Hauterivian ammonites from France richness repeatedly peaked during the TST, followed by nearly monospecific assemblages within the HST (Bulot 1993). Within the Upper Muschelkalk maximum richness is found in the HST of om9, and this increased richness is not the result of differences in sample size. Even factoring in the possibility of misidentification of some specimens, om9 would remain the most species-rich interval.

By abandoning the previously used subgenera, the taxonomic revision of Ulrichs (2006) reduces the radiation of *Ceratites* to a lower taxonomic rank (species-level). Yacobucci (1999) argued that radiations of taxa within epicontinental settings during transgressions would tend to be at lower taxonomic ranks and in response to the appearance of short-lived, unstable environments, with the origin of higher taxa during regressive phases when allopatry would be more likely. A ranking argument alone is not a strong line of evidence, but it should be noted that the radiation of *Ceratites* in the Upper Muschelkalk fits this scheme. Additional support for the ecological differentiation/speciation comes from two observations: (i) the high rate of speciation during the om7 and om8 intervals; (ii) the shift to RADs that are compatible with niche-partitioning, whether by speciation or immigration.

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Holland's (1995) simulation results placing the first occurrence of many taxa relatively soon after the beginning of new sequences are compatible, to some extent, with the findings of this study but in this case the sudden increase in absolute richness does not occur until towards the end of base-level rise. Two possible explanations exist for this observation. The first is that preservation/sampling of taxa does not increase uniformly during base-level rise. In this case the final, upper part of the TST may preserve more individuals and taxa, despite its shorter duration. Alternatively, the upper part of the TST does represent an interval when origination rates increased. As the number of occurrences drops slightly during the om8, with the number of localities remaining similar, the latter explanation does receive some support. Klug et al. (2005) noted that the maximum morphological change occurred between their units 9 and 10, which are the two uppermost units of the TST. This is when *C. enodis* and *C. laevigatus* appear in the basin alongside more ornamented taxa. While Klug et al. (2005) regarded these taxa were immigrants, a phylogenetic analysis (McGowan 2009) places *C. enodis* and *C. laevigatus* in relatively derived positions within the phylogeny, which is evidence that these taxa evolved within the Muschelkalk Basin. Future work on the evolution of *Ceratites* will combine these new phylogenies with the current dataset to gain further insight into the relative roles of phylogenetic, developmental and environmental controls on the evolution and palaeoecology of the group. Being able to resolve the stratigraphic occurrences to the finer intervals used by Klug et al. (2005) would also permit greater insight into the relationship between higher-order sequences and richness.

Conclusions

This new study of abundance data on the occurrence of *Ceratites* in the Germanic Basin indicates that the overall pattern of increasing species-richness through time is not dependent on sampling effort or geological biases at the scale of the whole basin. Analyses of the relationships between sampling effort and Muschelkalk outcrop occurrences at smaller scales recover the well-known positive relationship between the number of occurrences (individuals sampled) and species richness per sampling unit (Rosenzweig 1995; Hayek and Buzas 1997; Alroy et al. 2001, 2008; Magurran 2004). Indeed sampling effort really should be regarded as the null hypotheses for observed differences at local scales in the fossil record. The number of localities sampled is of less predictive value, indicating that taxa are widely distributed throughout the basin, and that there is limited evidence for segregation of taxa among localities, a conclusion further supported by the steady 50% similarity among sites observed among the three intervals. The amount of rock available to sample has a limited influence on richness, with much poorer predictive power for a single lineage within a restricted area than for overall marine invertebrate diversity at regional or global levels (Peters and Foote 2001, 2002; Smith et al. 2001; Crampton et al. 2003; Smith and McGowan 2007).

Although a shift to more stable ecosystems through time is congruent with previous work on the *Ceratites* assemblages, this shift is not accompanied by a change from a high to low degree of similarity among localities through time; average similarity between sites varied by only 3% during the Upper Muschelkalk. As speciation processes that relied upon either geographic isolation, or spatially discrete ecological resources would tend to decrease similarity among sites, speciation processes in the Upper Muschelkalk are either not detectable at this level of spatio-temporal resolution or are not primarily driven by gross geographic partitioning.

This study provides further support for the reality of an endemic radiation of *Ceratites* within the Muschelkalk Basin, with an overall pattern of relatively steady accumulation of richness, punctuated by an increase in richness during the om8 interval, accompanied by the appearance of the first compressed, weakly ornamented species towards the top of om8 approaching the maximum flooding surface of the Upper Muschelkalk. This may be evidence of the sudden emergence of new habitats during the final stages of onlap that then became widespread during the HST in om9.

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