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Fossils of Devonian ammonoids are abundant and well-preserved in the Anti-Atlas of Morocco; as such they provide an invaluable record of regional morphological disparity changes (diversity of shapes) that characterise the first steps of the ammonoid evolution. However, they were rarely analysed quantitatively with respect to their morphological spectrum. Here, we investigated the morphological disparity of the early ammonoids by analysing the shape of their whorl profile. A geometric morphometric approach based on the acquisition of outline semilandmark coordinates was used to analyse the whorl profiles. For comparison, morphometric ratios based on classical conch measurements were also analysed to investigate the overall conch geometry. Several standard disparity estimators were computed to measure different aspects of morphological disparity fluctuations through time. It appears that a major increase in disparity occurred throughout the Early Devonian, followed by ups and downs during the Middle Devonian constituting a general decreasing trend. Only the end-Eifelian Kačák event shows a significant decrease in disparity. Thus, the ammonoids explored the range of possible shapes fairly quickly during their initial radiation; however, we found no evidence for an early burst of shape diversity (i.e. the rise does not exceed the expectations given diversity). Nevertheless, correlation tests between diversity and disparity time series support that they are partially decoupled. The highly resolved biozone record

highlights that the increase in disparity began earlier than the increase in diversity that characterise the late Emsian.

Key words: macroevolution, morphological disparity, geometric morphometrics, ammonoids, Devonian, conch geometry

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Introduction

Ammonoids are extinct cephalopods with an external coiled conch; they originated in the Early Devonian (Schindewolf 1933; Erben 1953, 1960, 1964, 1965, 1966; Becker and House 1994; Klug et al. 2008b; De Baets et al. 2013; Becker et al. 2019). They descended from the Bactritida, which root in the latest Silurian or earliest Devonian Orthocerida (Erben 1966; Kröger and Mapes 2007; Klug et al. 2015). Thanks to their numerous morphological characters, ammonoids constitute an invaluable fossil record for documenting macroevolutionary patterns (e.g. Kennedy and Cobban 1976; Teichert 1986; House 1988; Brayard et al. 2009; Monnet et al. 2011; Korn and Klug 2012; Brosse et al. 2013; Tendler et al. 2015).

The initial radiation of ammonoids took place in a context of environmental conditions that were repeatedly affected by more or less severe crises (Klug et al. 2010). Several global events, usually associated with significant environmental changes, have been recorded by the

study of Devonian rocks and fossils. Some of these events severely impacted marine life and led to extinction phases (for a review of Devonian global events and crises, see Walliser 1984, 1996; House 1985, 1996a, 2002; Becker et al. 2016). House (1989), Saunders et al. (2008), Korn and Klug (2012) and Korn et al. (2015) documented changes in the taxonomic diversity of Palaeozoic ammonoids. For the time interval studied here (Early and Middle Devonian), global reductions in ammonoid diversity were recorded for the late Emsian Daleje Event, the end-Eifelian Kačák Event and the Givetian Taghanic Event (Korn and Klug 2012).

Taxonomic diversity trends can be compared to disparity (i.e. the diversity of phenotypes) trends; they provide a robust framework for discussing evolutionary processes and understanding biotic crises (Roy and Foote 1997). To achieve that, multivariate ordination methods allow to quantify morphological disparity and provide a convenient way to study the variation of shapes without considering the taxonomic or phylogenetic context (Foote 1997; Nardin et al. 2005). They have been successfully applied to various cephalopod groups, such as ammonoids (e.g. Dommergues et al. 1996; Simon et al. 2010; Korn and Klug 2012; Hoffmann et al. 2019), belemnites (Dera et al. 2016; Nätscher et al. 2021) and modern coleoids (Neige 2003; Hoffmann et al. 2021).

Classic methods involving linear measurements of the conch, as the so-called Raupian parameters (Raup and Michelson 1965; Raup 1966, 1967; Korn and Klug 2003), enable the calculation of morphometric conch properties. This traditional approach allows for the quantification of the entire conch geometry; however, it does not allow us to take into account all the morphological features that characterise the morphology of the conch, such as the degree of whorl overlap, the curvature of the flanks and the presence of grooves and keels (Korn and Klug 2012). Therefore, a geometric morphometric approach applied to the whorl profiles represents an alternative to complement the understanding of the conch shape evolution (Korn and Klug 2012). The shape of the whorl profile determines two dimensions

of the space that accommodated the animal's soft body (but not the length of the body chamber). The preparation of cross sections of ammonoid conchs is considered a classic method for studying this group and provides an immense amount of biometric data (Reyment and Kennedy 1991; Korn and Klug 2003; Korn and Klug 2012). The shape of the whorl profile is highly variable in ammonoids and it is therefore used in various studies investigating their changes in morphological disparity (e.g. Simon et al. 2010; Korn and Klug 2012; Klein and Korn 2014).

Several studies have already examined the morphological evolution of Devonian ammonoids – mostly on a global level (Korn and Klug 2003, 2012; Monnet et al. 2011; De Baets et al. 2012; Korn et al. 2015; Whalen et al. 2020). Through the Devonian, rapid coiling trends from uncoiled/straight ancestors to ammonoids with coiled embryonic as well as post-embryonic conchs have been documented (House 1996a; Korn and Klug 2003; Klug and Korn 2004; Klug et al. 2008b; Monnet et al. 2011; De Baets et al. 2012, 2013; Naglik et al. 2019). Korn and Klug (2012) and Korn et al. (2015) documented the fluctuations in morphological disparity through the Devonian using a standard morphometric method based on a modified version of the Raupian parameters (Korn 2010). They documented a major increase in morphological disparity during the Emsian, followed by a decrease from the Eifelian to the Givetian. Whalen et al. (2020) documented the global fluctuations of ammonoid disparity through the Palaeozoic based on conch morphometric data; in this study they used the ammonoids as a model taxon to test for the prevalence of early bursts (i.e. accumulation of morphological disparity in excess of taxonomic richness; see Simpson 1944; Foote 1994, 1997; Hughes et al. 2013; Benton et al. 2014). They also captured this pattern of rapidly increasing disparity through the Emsian; however, they found no evidence for an early burst: After being corrected for species richness, the disparity of Emsian ammonoids does not

exceed the null expectation given the concomitant increase in species richness (Whalen et al. 2020).

Furthermore, concerning the extinction events occurring through the studied time interval (Early and Middle Devonian), Korn and Klug (2012) and Korn et al. (2015) reported that only the end-Eifelian Kačák event was marked by a significant decrease in disparity; they found that changes in diversity and disparity were usually decoupled (Korn and Klug 2012; Korn et al. 2015). However, the results of Whalen et al. (2020) suggest that the majority of Palaeozoic ammonoid species-level morphological disparity could be explained by species richness alone, contrary to these previous works.

Korn and Klug (2012) were the only ones to investigate the morphological disparity of Devonian ammonoids by analysing the shape of the whorl profile using a Fourier analysis and a multivariate analysis; they described the evolution of the morphospace occupation at substage resolution. However, changes through time were not quantified using disparity indices. With their loosely coiled conchs (i.e. advolute/evolute conchs without whorl overlap), the early Emsian ammonoids occupied a very restricted part of the morphospace (Korn and Klug 2012). Then, a shift occurred and new shapes appeared through the late Emsian and the Middle Devonian, with a trend towards more involute conchs with increasing whorl overlap degrees (Korn and Klug 2012).

The purpose of our study is to accurately quantify the morphological disparity of ammonoids from their origination in the early Emsian (Early Devonian) to the end of the Givetian (Middle Devonian), by investigating the shape of the whorl profile using a geometric morphometric approach and standard disparity metrics. The novelty of our study also resides in the higher temporal resolution (biozone level), in the updated dataset including new data from all recent publications documenting early ammonoids from Morocco and from specimens prepared and drawn (DK). In addition, our study allows to test, at the regional

scale, the global findings of Whalen et al. (2020) concerning the relationship between morphological disparity and taxonomic richness and the occurrence of an early burst pattern. In this context, the highly resolved Moroccan biozone record enables to highlight changes that cannot be seen using a lower time resolution (i.e. substage or stage resolution).

Material and methods

Data compilation.—Our study is based on the fossil record of ammonoids from the Anti-Atlas of Morocco (Fig. 1), an area that is well-known for its abundant and well-preserved Devonian ammonoid assemblages. In the last decades, many papers documenting Early and Middle Devonian ammonoids from Morocco were published (Becker and House 2000; Klug et al. 2000, 2008b; Klug 2001a, b, 2002a, b, 2017; Becker et al. 2004, 2013, 2018, 2019; Becker 2007; Bockwinkel et al. 2009, 2013, 2015, 2017; De Baets et al. 2010; Aboussalam and Becker 2011; Ebbighausen et al. 2011). These studies provide a comprehensive and valuable record of taxonomic diversity and morphological disparity of ammonoids through time. Furthermore, working in this one area allows for the collection of data with a consistent species-level taxonomic framework and with a precise timescale based on the Moroccan ammonoid biozonation (Fig. 2). This time interval of around 22.3 million years (Walker et al. 2019) has been subdivided into 30 biozones based on ammonoids (Klug 2002a; Aboussalam and Becker 2011; Bockwinkel et al. 2015; Becker et al. 2019). In order to synthesise the more general changes in disparity observed at the biozone resolution and to visualise global trends, the studied time interval is divided into seven timeslices, which are also used as a time scale (Fig. 2).

The dataset analysed here is a compilation of drawings of whorl profiles (Fig. 3) from specimens illustrated in the literature (Chlupáč and Turek 1983; Korn 1999; Klug 2001a, 2002a; Korn and Klug 2002; Bockwinkel et al. 2009, 2013, 2015, 2017; De Baets et al. 2010; Aboussalam and Becker 2011; Ebbighausen et al. 2011; Becker et al. 2013, 2019) and from unpublished material (39 whorl profiles belonging to 20 species). The dataset includes 127 Early and Middle Devonian ammonoid species that were documented from the Anti-Atlas (dataset available as supplementary online material at https://datadryad.org/stash/share/XXXX; see SOM 1 and 2). Most taxa (~70%) are represented by several drawings of the whorl profile, which correspond to ontogenetic stages of individual specimens. The decision to select only one specimen per species is guided by the aim of focusing only on the interspecific variation and not intraspecific variation (e.g. De Baets et al. 2013; Hoffmann et al. 2019). Some of the species could not be included in our analysis because their stratigraphic distribution is unclear or because complete whorl profile outlines were not available.

Independently, the conch geometry was also analysed on the base of classical linear measurements of the conch (App. S1; for details, see Korn 2010). For most species (75%), the analysed measurements (dataset available as supplementary online material at https://datadryad.org/stash/share/XXXX; see SOM 3) correspond to the same specimens from which the whorl profiles were analysed. From these measurements (App. S1), five morphometric ratios were calculated (see Korn 2010): Conch width index (CWI = ww/dm1), umbilical width index (UWI = uw/dm1), whorl expansion rate (WER = $(dm1/dm2)^2$), whorl width index (WWI = ww/wh) and imprint zone rate (IZR = (wh-ah)/wh).

Geometric morphometrics.—In our study, the shape of the whorl profile is quantified using geometric morphometrics with the acquisition of semilandmark coordinates on the outline (for

a general overview of geometric morphometrics, see Adams et al. 2004, 2013; Zelditch et al. 2012). All the functions used here to perform geometric morphometric analysis are from the R package Momocs (version 1.4.0; Bonhomme et al. 2014). Drawings of whorl profiles are automatically digitised into a series of 200 curvilinear equally-spaced points on the outline, the semilandmarks (Gunz and Mitteroecker 2013), by using the function 'coo_interpolate'. The standardisation of semilandmark data to correct the size/scale, position/translation, and orientation/rotation of whorl profiles is performed as follow: (i) translation effect is removed by centering the outlines (i.e. placing all outlines around their centroid, which is the average point of all semilandmarks) using the function 'coo_center'; (ii) coordinates of each outline are scaled by their centroid size using the function 'coo_scale'; (iii) the starting point of each outline (i.e. point located at the intersection between the outline and the line passing by the centroid with an angle of $\pi/2$) is defined using the functions 'coo_intersect_angle' and 'coo_slide'. Then, superimposed coordinates are modeled into harmonic coefficients with an elliptical Fourier analysis (EFA) (Kuhl and Giardina 1982; Ferson et al. 1985; Crampton 1995; Lestrel 1997; Haines and Crampton 2000; Bonhomme et al. 2014) computed with the function 'efourier'. The number of harmonics to be used for the subsequent analyses is selected by default in the function to represent at least 99% of the cumulative Fourier harmonic power, in our case this was achieved with 6 harmonics. Our scripts are available online (https://github.com/sginot/Ammonoids_disparity).

Morphospaces and disparity metrics.—To study the shape changes and to quantify the morphological disparity in time series, the obtained Fourier coefficients are analysed using a principal component analysis; this creates a multidimensional empirical morphospace (Foote 1991; Budd 2021). In macroevolutionary approaches, various disparity indices have been used to assess the changes in morphological disparity based on morphospace occupation (Foote

1991, 1993; Wills et al. 1994; Ciampaglio et al. 2001; Wills 2001; Guillerme et al. 2020). The computation of different types of disparity indices (i.e. size, density and position) is essential to catch different aspects of morphological disparity fluctuations through time (Hopkins 2022). Here, morphological disparity changes over time are analysed using five indices: sum of ranges (SoR) and convex hull area (i.e., size-based disparity indices); sum of variances (SoV) and mean squared Euclidean distance from centroid (i.e., density-based disparity indices); and average displacement (i.e., position-based disparity index). Confidence intervals are computed by randomly resampling with replacement points in the morphospace (1000 iterations) and extracting the 2.5 and 97.5 percentiles of the distribution (Foote 1991). The partial morphological disparity (i.e. sum of mean squared Euclidean distance from centroid per superfamilies) is computed using the method of Foote (1993). Disparity indices are calculated for each of the seven studied intervals constituting the Early and Middle Devonian, as well as for each of the 30 biozones (Fig. 2). To compute disparity indices, we produced our own custom code (available at https://github.com/sginot/Ammonoids_disparity) based on formulas from Foote (1993), Wills et al. (1994), Wills (2001) and Guillerme et al. (2020). All analyses are calculated using the scientific environment R (version 3.3.0, R Core Team 2016).

In order to compare traditional morphometrics based on linear measurements of ammonoid conchs to geometric morphometrics, the five conch morphometry ratios are ordinated using a principal component analysis to produce another morphospace, which is quantified similarly to the EFA-based morphospace (see disparity indices above).

In addition, for the two datasets, we applied the model of Whalen et al. (2020) to investigate the relationship between disparity and diversity, and to test the occurrence of an early burst pattern. This approach allows us to compare the measured disparity (estimated using the convex hull area calculated for PC1 and PC2) with the expected disparity corrected for species richness computed by applying the null model of Whalen et al. (2020). This null

distribution of disparity values is basically computed from iterated shuffling of the morphospace, which maintains the number of points for each time bin, but modifies the corresponding points by randomly assigning real data values to different taxa. For details, see the original article and our custom code.

Results

Morphospace and morphological changes.—The two first principal components for the whorl section profiles explain 95.7% of the total variance (PC1 = 67.3%; PC2 = 28.4%; Fig. 4). Along the first axis, the shape variation is associated with the degree of whorl compression, which corresponds to the relative width of the whorl profile compared to its height. The distribution of the whorl profiles along PC1 covaries with the whorl width index (WWI; see App. S2). Low PC1 values represent more compressed whorl profiles (whorl higher than wide, low WWI); towards high PC1 values, the whorl profiles are increasingly depressed (whorl wider than high, high WWI) (Fig. 4, App. S2). Along the second axis, shape variation is related to the degree of whorl overlap. The distribution of the whorl profiles along PC2 covaries with the imprint zone rate (IZR; see App. S2). Low PC2 values represent a lower overlap (more evolute conchs, low IZR); towards high PC2 values, the degree of overlap is increasing (more involute conchs, high IZR) (Fig. 4, App. S2). In summary, morphological gradients can be seen along PC1 and PC2, respectively, from compressed to depressed whorl profiles (PC1), with a very low to very high degree of overlap (PC2).

Considering the Emsian as a whole, the occupied morphospace already shows a wide range of morphologies, from very compressed to very depressed, with a degree of overlap from absent (gyroconic and advolute conchs) to moderate (subinvolute conchs) (Figs 4–5).

However, the morphospace occupation is rather low in the first Emsian interval (EMS-1, Fig. 6; biozones 1 to 3, App. S3), which is only produced by the ancestral ammonoid superfamily Mimosphinctoidea. The species of this superfamily show a very small range of morphologies (Fig. 6), usually with a compressed whorl profile and without whorl overlap (gyroconic to advolute conchs). During the second Emsian interval (EMS-2, Fig. 6; biozones 4 to 6, App. S3), the morphospace occupation increased, caused by the emergence of the Mimagoniatitoidea, which are characterised by a wider morphological spectrum. Their diversification led to an expansion of morphospace to both higher and lower PC1 values (more compressed/more depressed whorl profiles), and towards slightly higher PC2 values (higher overlapping degree). The last Emsian interval (EMS-3, Fig. 6; biozones 7 to 9, App. S3) records a significant increase in morphospace occupation. While the Mimosphinctoidea disappeared, the morphological range of the Mimagoniatitoidea increased and the Anarcestoidea appeared with their wide broad morphological spectrum (Fig. 6).

During the Eifelian, a large part of the total morphospace was occupied; even after the disappearance of the most compressed early Emsian forms, leaving the bottom-left corner of the morphospace unoccupied (Figs 4–5). The first Eifelian interval (EIF-1, Fig. 6; biozones 10 to 15, App. S4) shows an expansion of the morphospace towards lower PC1 scores, caused by the emergence of the Agoniatitoidea, which mainly explored the middle left part of the morphospace. This means that new shapes with very compressed whorl profiles and a higher degree of overlap appeared (Figs 4–6). Very involute forms characterised by a very high overlap degree, causing a horseshoe-shaped whorl profile, appeared within the Agoniatitoidea (top-most part of the morphospace; Fig. 6). During the second Eifelian interval (EIF-2, Fig. 6; biozones 16 to 19, App. S4), morphospace occupation became more restricted with the extinction of the Mimagoniatitoidea. The origination of the Tornoceratoidea did not lead to

any changes in the morphospace; they plot in the same area with some species of the Agoniatitoidea and the Anarcestoidea (Fig. 6).

During the Givetian, the density of documented shapes in the morphospace increased significantly towards high PC2 scores (Fig. 5), highlighting the diversification of forms characterised by a higher degree of overlap (Fig. 4). With the disappearance of the most compressed forms of the Agoniatitoidea, the middle left-most part of the morphospace became empty (Figs 4–6), while new forms characterised by more depressed whorl profiles diversified (expansion of the distribution towards lower PC1 scores; Fig. 6). The most depressed forms that were present during the Eifelian disappeared with the disappearance of the Anarcestoidea; however, they are partially replaced by the Pharciceratoidea, which occupied a large part of the morphospace during the Givetian (intervals GIV-1 and GIV-2, Fig. 6). The Pharciceratoidea emerged in the first Givetian interval (GIV-1, biozones 20 to 24; Fig. 6, App. S5), where they were already characterised by a wide range of morphologies, particularly in the degree of whorl overlap (Fig. 6). In addition, the new superfamily Gephuroceratoidea appeared; they are located in the same area as the Agoniatitoidea, but possessed a smaller range of morphology (Fig. 6). The Tornoceratoidea still occupied a restricted part in the morphospace where they cluster in the central area. During the second Givetian interval (GIV-2, biozones 25 to 30; Fig. 6, App. S5), the Pharciceratoidea distribution generally expanded towards lower PC1 values, due to the presence of more compressed forms. The Tornoceratoidea diversified and occupied a larger part of the morphospace by expanding their distribution towards higher PC1 and PC2 values (Fig. 6). While the area occupied by the Agoniatitoidea decreased, the area occupied by the Gephuroceratoidea expanded and they showed a relatively large range of morphologies.

In summary, a progressive trend towards a higher overlapping degree is observed in the ammonoids from the Emsian to the Givetian (Figs 4–5). During the three stages, the density is

relatively high towards high PC1 values (0.2–0.4), and towards moderate to low PC2 values (-0.2–0.0) (Fig. 5); this trend underlines the dominance of moderately depressed whorl profiles with a moderate degree of overlap (average morphology in terms of compression and overlap).

Morphological disparity trends.—The squared Euclidean distance and the SoV (density-based disparity indices; Figs 7–8) show a long increasing trend from the early Emsian to the late Eifelian, followed by a slow decrease until the late Givetian where moderate disparity values are recorded.

The sum of ranges (i.e. size-based disparity indices)) also records a progressive increase from the Emsian to the Eifelian, with very high values being reached in the first Eifelian interval. Then the disparity significantly decreased and reached moderate values in the first Givetian interval, to finally increase in the second Givetian interval to reach a level slightly lower than the Eifelian maximum (Fig. 8).

The position based disparity index (average displacement = average distance from centre; Fig. 8) records high values during the two first Emsian intervals, then the values decreased and remained relatively low through the Eifelian and Givetian. This trend reflects the morphospace occupation change occurring through the late Emsian: with the appearance of new conch shapes the ammonoids started to explore the central part of the morphospace (Fig. 6). In other words, the early Emsian ancestral shapes do not constitute an average morphology from which the diversification occurred in all directions; we rather have an oriented diversification towards positive values of PCs 1 and 2 (see Fig. 6).

In summary, in terms of density and size, a global rise in disparity is recorded from the Emsian to the Eifelian, followed by a decreasing trend occurring from the Eifelian to the Givetian (Figs 7–8). Variations at the biozone resolution show the same global trends (Figs 9–

10). The relatively high disparity recorded in the last Emsian interval (Figs 7–8) results in part from the ammonoid species occurring in the *Sellanarcestes wenkenbachi* Zone (biozone 8; Figs 9–10), where a large area of the morphospace is occupied (App. S3). The peak in the first Eifelian interval mainly results from the disparity recorded in the *Cabrieroceras* zones (biozones 14 and 15; Figs 9–10, App. S4). During the Givetian, the highest levels of disparity are recorded in late Givetian biozones (Figs 9–10, App. S5).

Some peaks result from the co-occurrence of superfamilies with different morphologies (e.g. Anarcestoidea and Agoniatitoidea during the Eifelian; Agoniatitoidea, Gephuroceratoidea and Pharciceratoidea during the Givetian; Figs 6–7, 9), while others are associated with the predominance of one superfamily with an important morphological variation (e.g. Mimagoniatitoidea during the second Emsian interval; Figs 6–7, 9).

Early burst pattern and correlation between disparity and diversity—To test for the occurrence of an early burst of shape diversity, we applied the approach proposed by Whalen et al. (2020). This approach allows to compare the measured disparity estimated using the convex hull area computed for PCs 1 and 2, with the expected variations of this index calculated considering the number of species in each bins (i.e. null model; Fig. 11). The measured values of this disparity estimator show similar variations as the SoR (Figs 8, 10, 11), since they both constitute size-based disparity indices. Despite the rapid increase in disparity recorded through the Emsian, the results do not suggest any evidence for an early burst: The disparity of Emsian ammonoids from Morocco does not exceed the null expectation given the concomitant increase in taxonomic diversity (Fig. 11). It is in fact generally lower than expected considering a null hypothesis of random appearance of new morphologies in the morphospace.

Correlation tests between the disparity indices and the number of species (diversity) were assessed using Pearson's approach (Haining 1991; Pearson 1896); the data were detrended using the method of Graeme T. Lloyd (https://www.graemetlloyd.com/methgd.html) before testing correlations (results of the correlations tests are available in App. S6). At the interval resolution (N=7), the correlation tests fail to find significant correlation between species disparity and species diversity for all indices (all p-values > 0.05; see App. S6). At the biozone resolution (N=30), the size-based disparity indices (i.e. sum of ranges and convex hull area) show significant correlations with the number of species (p-values << 0.010; see App. S6); while for the other indices (i.e., sum of variances, squared Euclidean distance and average displacement) the correlation tests fail to find a significant correlation with diversity (all p-values > 0.05; see App. S6).

Impacts of Early and Middle Devonian events.—The Upper Zlíchov Event (late early Emsian) is associated with a global minor transgression and with the spreading of hypoxic conditions (García-Alcalde 1997; Becker and Aboussalam 2011; Ferrova et al. 2012, 2013; Aboussalam et al. 2015). In Morocco, this event correlates with moderate disparity values and low taxonomic richness (Figs 9–10).

The Daleje Event (early late Emsian) corresponds to global sea level rise (House 1985, 2002; Ferrova et al. 2012, 2013; Aboussalam et al. 2015). Although the last representatives of the Mimosphinctoidea became extinct during this global transgressive event, diversity increased with the emergence of the Anarcestoidea (Figs 9–10). In terms of disparity, the size-based indices (i.e. sum of ranges and convex hull area, Figs 10–11) record a significant increase. The density-based disparity estimators (i.e. sum of variances and squared Euclidean distance) also show a slight increase but not significant. The average displacement decrease

considerably and significantly through this time interval, reflecting the important change in morphospace occupation (App. S3).

The Choteč Event (early Eifelian) is associated with a pulse of eutrophication and with an important turnover observed in many groups of organisms (Chlupáč and Kukal 1986, 1988). Impressive evidence of sudden flooding associated with anoxic facies was documented in the Anti-Atlas of Morocco (Becker and House 1994, 2000; Becker and Aboussalam 2013). In this time interval, the taxonomic richness is rather moderate. The disparity is relatively high in terms of size and density, but low in terms of position; no significant changes are recorded (Figs 9–11).

The Kačák Event (latest Eifelian) is a global extinction event (major marine faunal turnover) considered to be caused by climate change (House 1996b, 2002; Suttner et al. 2017). An occurrence of black shales associated with widespread hypoxic/anoxic conditions was documented (Suttner et al. 2017). The species diversity of the Moroccan ammonoids decreased drastically after the Kačák events. In terms of morphological disparity fluctuations, the size-based indices record a significant decrease after the Kačák Event (Figs 10–11); the density-based indices also show a decrease, but very slight and not significant (Figs. 9–10). The morphospace occupation become restricted after the Kačák Event (compare the two last Eifelian biozones with the first Givetian one, Apps S4–S5). Interestingly, the decrease in disparity appears less sharp than the decrease in diversity.

The Taghanic Event (middle–late Givetian) corresponds to a multi-phased global crisis that led to major turnover in many groups of organisms (House 2002; Aboussalam and Becker 2011; Turnau 2014; Maillet et al. 2015; Narkiewicz et al. 2016). Like other events, it is associated with sudden climate changes including greenhouse overheating pulses and sea level fluctuations (Aboussalam and Becker 2011; Zambito et al. 2012). In the Anti-Atlas, no

significant changes are recorded in terms of both diversity and disparity; both remain relatively stable during this time interval (Figs 9–11).

Discussion

The major pattern highlighted by the geometric analysis of ammonoid whorl profiles is a rapid increase in the range of whorl profile disparity in early ammonoid evolution, reaching a stabilisation in the late Emsian to early Eifelian (i.e. see size and density disparity metrics; Figs 7–11). This might be related to the rapid morphological evolution from loosely coiled or advolute conchs to those with increasingly overlapping whorls (Klug and Korn 2004; De Baets et al. 2012, 2013). This is consistent with the variations of the position-based disparity estimator; a shift is visible between the Emsian and the rest of the studied time interval (Fig. 10). This trend towards a higher degree of whorl overlap continued throughout the Givetian, where the involute forms with high whorl overlap are more diverse (Fig. 5).

The morphospace based on the conch morphometry ratios (App. S7) also highlights that ammonoids already displayed a wide range of morphologies in the Emsian; this also shows a trend towards a higher degree of whorl overlap from the Early to the Middle Devonian (i.e., exploration of the bottom-left part of the morphospace through the Middle Devonian corresponding to the appearance of more involute conch with a higher degree of overlap, App. S7). Comparing the disparity based on whorl profile and conch morphometry ratios, respectively, the same general trends are observed (Fig. 8, App. S8). At the interval resolution, the size and density-based disparity estimators show a rapidly increasing disparity through the Early Devonian followed by a moderate and relatively progressive decrease through the Middle Devonian (Fig. 8, App. S8); the position-based disparity estimator shows

high values in the two first Emsian intervals, then the values decrease significantly and stay low during the Middle Devonian (Fig. 8, App. S8). Despite these similar general trends, however, differences can be recognised: regarding the size-based disparity indices, the conch ratio disparity had an earlier maximum (late Emsian) than the whorl profile disparity (early Eifelian) (compare the variations of the sum of ranges and convex hull area for the whorl profiles and conch morphometry ratios, respectively; Figs 8, 11, Apps S8, S9). The Agoniatitoidea that emerged through the early Emsian are characterised by a wide range of whorl profile shapes, while range in terms of conch morphometry ratios (overall shape of the conch) is more restricted. With its extreme shape, *Mimotornoceras djemeli* (represented by the topmost dot in the morphospace), contributes clearly to the high disparity values recorded in the first Eifelian interval (Fig. 8).

In ammonoids, the loosely coiled conch constitutes the plesiomorphic state of morphology, since they are interpreted to have descended from bactritoid ancestors with straight conical or slightly curved conchs (Schindewolf 1933; Erben 1964; Korn 2001; Klug and Korn 2004; Kröger and Mapes 2007; Klug et al. 2015; Cichowolski and Rustán 2017). De Baets et al. (2012) documented the simultaneous increase in coiling of the inner whorls and the disappearance of the umbilical window in several Early Devonian ammonoid lineages. These trends, as well as the trend towards a higher degree of whorl overlap in the adult stage, may have affected the swimming capabilities and fecundity in ammonoids (Klug and Korn 2004; De Baets et al. 2012). The repeated coiling trends might be a response to increased predatory pressure as proposed for various molluscs groups (e.g. Nützel and Frýda 2003; Kröger 2005; De Baets et al. 2012, 2013; Klug et al. 2017; Dzik 2020). During the Devonian, various predatory groups capable of preying on ammonoids were already well established (Whalen and Briggs 2018; Ferrón and Donoghue 2022). The ammonoid conch geometry can be interpreted as the result of tradeoffs between different functional ecological tasks (e.g.

hydrodynamics, economy of shell material, shell growth, compactness) (Tendler et al. 2015, see also Hebdon et al. 2022).The loosely coiled conch was considered as an optimised morphology for an economy of shell material (Tendler et al. 2015). However, they are mechanically weaker and hydrodynamically less favourable; they can be crushed more easily by predators than tightly coiled conchs (Brett and Walker 2002; Nützel and Frýda 2003; Kröger 2005; Wagner and Erwin 2006; Klug 2007; De Baets et al. 2012). Following this idea, this trend towards increased coiling of the conch was usually interpreted as the result of adaptative pressures coupled with improved hydrodynamics. This allows for a higher swimming velocity and improved manoeuvrability (Chamberlain 1976, 1981; Klug 2001a; Korn and Klug 2003; Klug et al. 2008a, b, 2016; Monnet et al. 2011; De Baets et al. 2013; Frey et al. 2014; Naglik et al. 2015; Tendler et al. 2015), providing an advantage to escape from predators. The diversification of vertebrate nektonic predators, including fishes, and the escalation of their swimming capabilities was more complex and gradual than previously understood (Klug et al. 2010, 2017; compare with Whalen and Briggs 2018, and Ferrón and Donoghue 2022). Nevertheless, various or repeated pulses of increase in coiling may have occurred in conjunction with radiation pulses of active predators (Kröger 2005). But other factors might be involved; increased coiling also correlates with increasing fecundity as well as decreasing embryo size, leading to an increase in reproductive rates (Klug 2001*a*, 2007; De Baets et al. 2012, 2013, 2015; compare Ritterbush et al. 2014). It appears likely that tighter coiling enhanced swimming and reproductive capabilities of these cephalopods. However, this evolutionary tendency could be also driven by competition in a diversity-saturated habitat together with availability of abundant planktonic food (e.g., Klug et al. 2010) while the radiation of nekton might have been more smeared out (Whalen and Briggs 2018, and Ferrón and Donoghue 2022). It has at least been plausibly suggested that many ammonoids, compared to other pelagic groups, had a more passive life history with reduced mobility

potential and reduced capacities for larger prey items based on their small estimated buccal masses and hyponomes (Walton and Korn 2018).

The changes in conch morphology of early ammonoids occurred simultaneously and convergently (or even in parallel) in various taxa (Korn and Klug 2003; Kröger 2005; Monnet et al. 2011, 2015; De Baets et al. 2013; Klug et al. 2015; Naglik et al. 2019). This supports the hypothesis that the evolutionary trend towards more densely coiled conchs was ecologically driven. In any case, the change in coiling modified the *syn vivo* shell orientation in such way that the aperture became horizontally aligned with the centre of mass, enabling the ammonoids having higher swimming speeds (Saunders and Shapiro 1986; Klug 2001a; Klug et al. 2008b; Hoffmann et al. 2015; Naglik et al. 2015).

Independent of these adaptative explanations, morphological changes of the early ammonoid conchs might also have resulted from a random walk biased by left-wall effects (i.e. constructional constraints; Monnet et al. 2011, 2015). In that case, the hypotheses about ecological trends mentioned above just describe side-effects of other trends; but all these explanations may also have worked in concert.

Regarding disparity patterns, Korn and Klug (2012) documented an important increase through the Emsian followed by a sharp decrease during the Eifelian and Givetian. This result was based on linear (conch) measurements. Our geometric morphometric analysis of whorl profiles also captures this general pattern of decreasing disparity through the Middle Devonian, but the drop down is not that sharp and we can see that the disparity has rather decreased moderately and progressively after the rapid increase observed during the Emsian (see the fluctuations at the interval resolution, Figs 7–8). The significant increase in disparity occurring during the Emsian is recorded based on both conch morphometry ratios and whorl profiles (Fig. 8, App. S8); therefore, in the initial phase of their evolutionary history, the ammonoids rather quickly explored the range of available shapes. Interestingly, we can see

that this increase began even earlier than the increase in taxonomic diversity that characterises the late Emsian (Figs 7–10). The results of Whalen et al. (2020) show high disparity levels in the evolution of the late Emsian and earliest Givetian ammonoids. Our results corroborate the high disparity reached in the late Emsian, but do not show any disparity pike in the earliest Givetian (Fig. 10); for the Moroccan ammonoids the disparity rather increased later in the late Givetian, and also reached a high level in the Eifelian (Fig. 10).

Our results confirm that the ammonoids reached a high disparity early in their evolution. However, according to the results obtained by applying the test of Whalen et al. (2020) for early burst evolution, this rise does not exceed the expectations given diversity (for the whorl profiles as well as for the conch morphometry ratios; Fig. 11, App. S9). In fact, disparity is consistently lower than the values expected under the null distribution. This may suggest that this test is overly conservative. Indeed, this might be explained by the fact that the null distribution is produced under the assumption that any (really sampled) morphology may appear in the morphospace, no matter what the morphospace of the previous time interval was. Therefore, morphologies differing completely from their putative ancestral stock of species are allowed to appear, potentially producing an overestimate of disparity, when compared for example to a Brownian motion. Under Brownian motion, the test of Whalen et al. (2020) would have to be modified to account for the fact that new morphologies are less likely to appear further away from standing morphologies. Such modification would certainly decrease the distribution of disparity values, and render the test less conservative. Notwithstanding these criticisms, as it stands, the test does not allow us to state firmly that the early increase in disparity observed in ammonoids corresponds to an early burst pattern or not. Although the ‘early high disparity’ model has been documented for many animal clades (Foote 1994, 1997; Erwin 2007; Hughes et al. 2013; Benton et al. 2014; Oyston et al. 2015; Wagner 2018), it seems that this trend is not the predominant pattern throughout the

Phanerozoic and that is even rather rare (Whalen et al. 2020).The development of a less conservative test for this pattern, although not the aim of the current paper, might help solve this open debate on the frequency of early burst patterns through evolution.

The complex relationship between taxonomic diversity and morphological disparity has been widely investigated and debated; some studies showed a decoupling (e.g. Fortey et al. 1996; Bapst et al. 2012; Missagia et al. 2023) while others demonstrated that the two signals could be coupled (e.g. Whalen et al. 2020; Bault et al. 2023). For our two analyses, whorl profiles and conch morphometry ratios, correlations between taxonomic diversity and the size-based disparity indices (i.e., sum of ranges and convex hull area for PCs 1 and 2) are evidenced at the biozone resolution; but for all other indices correlation tests failed to find correlation with the number of species at both the interval and biozone resolutions (App. S9). According to our results, it appears that diversity and disparity are partially decoupled; this may be dependent on the type of indices used. As such, studies investigating these correlations might benefit from systematically including several of these indices.

Conclusions

The disparity signal is complex, and different patterns can be caught depending on what type of index we are looking at. According to the size and density-based disparity estimators, a significant rise in ammonoid disparity occurred during the Early Devonian, confirming that ammonoids achieved high disparity levels early in their evolutionary history. Nevertheless, according to the test carried out, we found no evidence for an early burst pattern in the regional disparity dataset: the measured disparity does not exceed the expectations of the null model, which may however be too conservative. The position-based disparity index shows a distinct pattern, compared to the other indices; a sharp decrease is recorded from the early to

the late Emsian, reflecting a shift in the morphospace occupation. Thereafter, the disparity shows ups and downs following a general moderately decreasing trend trough the Middle Devonian. Among the events occurring during the studied time interval, just the Kačák Event appears to have impacted the disparity, but only partly: the size-based disparity estimators record a significant decrease after the event, however, the other type of indices do not show significant fluctuations. Diversity and disparity appear partially decoupled (i.e. correlation tests only reveal significant correlations for the size-based disparity indices, at the biozone resolution). From the Early to the Middle Devonian, a progressive trend towards a higher degree of whorl overlap is recorded. The involute conchs with a high whorl overlap are particularly abundant in the Givetian; the involute morphologies correspond to shapes interpreted to be optimised for hydrodynamic efficiency allowing improved swimming abilities (Tendler et al. 2015; Klug et al. 2016). This pattern fits well with the presence of nektonic predators that were already well established during the Devonian, which may have induced a selective pressure in favour of tighter coiled conchs, more suited to changing environments than the Emsian loosely coiled relatives that finally disappeared. The shift recorded by the position-based index through the Early Devonian reflects this transition towards more involute conchs.

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Appendices

Appendices (table and supplemental figures) can be found in the online version of this article: Appendices S1–S9.

Supplemental Online Material

Data for this study [SOM 1–3] are available in the Dryad Digital Repository: https://datadryad.org/stash/share/XXXX [please note that the data for this paper are not yet published and this temporary link should not be shared without the express permission of the author]

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FIGURE CAPTIONS

Fig. 1. Simplified geological map of Morocco (modified from Klug 2002a).

Fig. 2. Stratigraphic scheme for the Early and Middle Devonian of the Anti-Atlas of Morocco, showing the distribution of superfamilies through time. Ammonoid biozonation from (Klug 2002a; Aboussalam and Becker 2011; Bockwinkel et al. 2015; Becker et al. 2019). Absolute

ages from the Geological Time Scale v. 5.0 (Walker et al. 2019). *Sobolewia* n. sp. and *Afromaenioceras* n. sp. have been introduced by Becker et al. (2004), and *Lunupharciceras* n. sp. by Aboussalam and Becker (2011); these new taxa have not yet been formally described but they are mentioned in several studies where they are used to establish the biozonation (e.g. Becker et al. 2004; Aboussalam and Becker 2011).

Fig. 3. Ammonoid morphology and dataset. A, Morphology of an ammonoid; as an example, the outline of the whorl profile taken at the maximum conch diameter is highlighted in red (modified from De Baets et al. 2010). B, Dataset analysed here; compilation of drawings of whorl profile outlines corresponding to Early and Middle Devonian ammonoids from Morocco.

Fig. 4. Morphospace occupation observed for the Early and Middle Devonian, based on the analysis of the whorl profiles, with representative examples of shapes. The first two axes explain 95.7% of the variance.

Fig. 5. Diagrams showing the morphospace occupation observed for the three stages constituting the Early and Middle Devonian, with level contours and density curves; based on the analysis of the whorl profiles.

Fig. 6. Evolution of the morphospace occupation through the seven intervals constituting the Early and Middle Devonian, showing the distribution of ammonoid superfamilies; based on the analysis of the whorl profiles. See Fig. 2 for interval labels.

Fig. 7. Relative contribution of ammonoid superfamilies to diversity and disparity (squared Euclidean distance); based on the analysis of the whorl profiles. See Fig. 2 for interval labels.

Fig. 8. Evolution of disparity through the Early and Middle Devonian (estimated by sum of ranges, sum of variances and average displacement); based on the analysis of the whorl profiles. Error bars are computed after 1000 bootstraps. The sampled-in-bin diversity is indicated in blue bars. See Fig. 2 for interval labels.

Fig. 9. Evolution of the relative contribution of ammonoid superfamilies to diversity and disparity (mean squared Euclidean distance to the centroid) through the Early and Middle Devonian ammonoid zones (biozones numbered from 1 to 30, see Fig. 2); based on the analysis of the whorl profiles.

Fig. 10. Evolution of disparity through the 30 studied biozones representing the Early and Middle Devonian (estimated by sum of ranges, sum of variances and average displacement); based on the analysis of the whorl profiles. Error bars are computed after 1000 bootstraps. The sampled-in-bin diversity is indicated in blue bars.

Fig. 11. Variations of the convex hull area computed for PCs 1 and 2, based on the analysis of the whorl profiles through the Early and Middle Devonian. Comparison of the measured values with the expected values given diversity, computed by applying the null model of Whalen et al. (2020).

APPENDICES CAPTIONS

Appendix S1. Linear measurements used to compute the conch morphometry ratios: Conch Width Index (CWI = ww/dm1), Umbilical Width Index (UWI = uw/dm1), Whorl Expansion Rate (WER = $(dm1/dm2)^2$), Whorl Width Index (WWI = ww/wh) and Imprint Zone Rate (IZR = (wh-ah)/wh).

Appendix S2. Crossplots showing the distribution of the whorl profiles along the first (PC1) and the second axes (PC2) of the PCA, depending of the imprint zone rate (IZR) and the whorl wide index (WWI).

Appendix S3. Evolution of the morphospace occupation through the nine ammonoid zones constituting the Emsian of Morocco; based on the analysis of the whorl profiles.

Appendix S4. Evolution of the morphospace occupation through the 10 ammonoid zones constituting the Eifelian of Morocco; based on the analysis of the whorl profiles.

Appendix S5. Evolution of the morphospace occupation through the 11 ammonoid zones constituting the Givetian of Morocco; based on the analysis of the whorl profiles.

App. S6. Table showing the results of the Pearson's correlation tests.

Appendix S7. Morphospace occupation observed for the Early and Middle Devonian, based on the analysis of the conch morphometry ratios (CWI, UWI, WER, WWI, IZR), with representative examples of shapes. The first two axes explain 85.9% of the variance.

Appendix S8. Evolution of disparity through the Early and Middle Devonian (estimated by mean pairwise distance, sum of ranges and sum of variances); based on the analysis of the conch morphometry ratios (CWI, UWI, WER, WWI, IZR). Error bars are computed after 1000 bootstraps. The sampled-in-bin diversity is indicated in blue bars. See Fig. 2 for interval labels.

App. S9. Variations of the convex hull area computed for PCs 1 and 2, based on the analysis of the conch morphometry ratios through the Early and Middle Devonian. Comparison of the measured values with the expected values given diversity, computed by applying the null model of Whalen et al. (2020).