ABHANDLUNGEN DER GEOLOGISCHEN BUNDESANSTALT

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Conch Parameters and Habitats of Emsian and Eifelian Ammonoids from the Tafilalt (Morocco) and their Relation to Global Events

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16 Text-Figures

Morocco
Devonian
Emsian
Eifelian
Ammonoidea

Contents

Gehäuse-Parameter und Lebensräume von Ammonoideen der Ems- und Eifel-Stufe aus dem Tafilalt (Marokko) und ihre Beziehungen zu globalen Meeresspiegelschwankungen

Zusammenfassung

Maximale Gehäusedurchmesser, Windungsexpansions-Raten und Windungsbreiten-Durchmesser-Verhältnisse wurden von 500, den Sedimenten der oberen Ems- und Eifel-Stufe von fünf Aufschlüssen im Tafilalt (Marokko) horizontiert entnommenen Ammonoideen gemessen (Unterordnungen Agoniatitina und Anarcestina). Die sedimentologischen Parameter wie Korngrößen und Mikrofazies wurden untersucht und mit Hilfe der Litho- und Biostratigraphie der Profile mit globalen Meeresspiegelkurven korreliert. Aus der Korrelation der Gehäuseparameter-Variation mit Meeresspiegelschwankungen konnten die folgenden Rückschlüsse auf die Lebensräume der untersuchten Ammonoideen gezogen werden: Die eher schmalen, brevidomen Gehäuse der verhältnismäßig großen Agoniatiten hatten hohe Windungsexpansions-Raten und wurden überwiegend in Sedimenten aus geringeren Wassertiefen gefunden. Die kleineren, longidomen Gehäuse der Anarcestiden haben niedrigere Windungsexpansions-Raten und wurden meist etwas tiefer marinen Ablagerungen entnommen. In diesen Sedimenten, die während Transgressionen oder Meeresspiegel-Hochständen abgelagert wurden, weisen die Gehäuse im Durchschnitt geringere Gehäusedurchmesser auf. Zudem enthalten die meisten Ammonoideen führenden Schichten entweder nur Gehäuse von Agoniatitina oder ausschließlich von Anarcestina. Wiederholte Fluktuationen in den Gehäuseparametern und im Verhältnis von Agoniatitina zu Anarcestina werden durch Wanderungen von Populationen der beiden Taxa in Abhängigkeit von Änderungen der Bathymetrie oder anderer Umweltfaktoren wie dem Sauerstoffgehalt des Wassers erklärt .

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Abstract

Maximal conch diameters, whorl expansion rates, and whorl width/diameter ratios of 500 in situ collected late Emsian and Eifelian ammonoids (suborders Agoniatitina and Anarcestina) from five localities in the Tafilalt (Morocco) were measured and calculated. Lithology, grainsizes, and microfacies of the sections were investigated and correlated with global sea-level curves using litho- and biostratigraphy. From the correlation of variations in the ammonoid conch parameters with sea-level alternations, the following conclusions on ammonoid habitats were drawn: The slender brevidomic conchs of the relatively large agoniatids have high whorl expansion rates and were predominantly found in deposits from shallow water environments. The longidomic and smaller conchs of the anarcestids show low whorl expansion rates and were mostly found in sediments which were deposited during transgressive phases or sea-level high stands. However, conchs with small diameters and low whorl expansion rates do not display a clear correlation with sea-level changes. Additionally, most samples contain either exclusively representatives of the Agoniatitina or of the Anarcestina. Rapid fluctuations in the conch parameters and synchronously in the Agoniatitina/Anarcestina ratio are interpreted as the result of migrations of populations of the two taxa which depended on bathymetry or other environmental factors such as oxygenation of bottom waters, shifting with varying sea-level.

1. Introduction

Most investigations on ammonoid ecology have focused on a comparison with Recent *Nautilus* (e.g. WARD & WESTERMANN, 1985), or the correlation between taxonomic units (ZIEGLER, 1967; MARCHAND, 1992) or "morphotypes" (BATT, 1989; BECKER, 1996a,b; WIESE, 1999) with sedimentological data of the studied sections and associated faunas. Information about the ammonoid habitats were often extracted from conch hydrostatics or hydrodynamics (WESTERMANN, 1971, 1973, 1982, 1987, 1996; TANABE, 1979; WARD & WESTERMANN, 1985; HEWITT & WESTERMANN, 1986, 1987, 1997; TSUJITA & WESTERMANN, 1998; WESTERMANN & TSUJITA, 1999). KEUPP (1984/85, 1999) used the distribution of pathologies to reach conclusions on the properties of the habitats of Jurassic ammonoids. NEIGE et al. (1997) correlated variations in the morphospace occupied by Middle Jurassic ammonoids with eustatic trends. Correlations of sedimentological cycles with "iterative morphological cycles" were discovered by BAYER & MCGHEE (1985) in ammonoid associations of the German Jurassic. STEVENS (1988) and MANGER et al. (1999) focused on occurrences of giant ammonoids and compared ammonoid gigantism with recent giant squids. In the present study, simple conch parameters such as the maximal diameter (KLUG, 1999a,b), whorl expansion rate and whorl width/diameter ratio are correlated with changes in the accompanying fauna, sea-level curves, the microfacies, and the grainsize in order to study the ecological demands of the Devonian ammonoid suborders Agoniatitina and Anarcestina.

The rich occurrences of Devonian ammonoids in Northwest Africa are some of the most fossiliferous localities with sedimentary rocks of this age. Many of the localities have been known since CLARIOND (1935) but our knowledge of the ammonoid faunas is based principally on the monographs of TERMIER & TERMIER (1950) and PETTER (1959). The importance of the Northwest African and in particular of the Moroccan Emsian and Eifelian sedimentary successions is due to the large and highly fossiliferous exposures of the eastern Anti-Atlas. Among these, the Ouidane Chebbi section, located 44 kilometres east of Erfoud and 30 km east of the Derkaoua oasis (Text-Figs. 1,5,8), is an excellent section for the study of late Emsian and Eifelian goniatites within a stratigraphical context (KLUG, 1998; BELKA et al., 1999). Nearby sections at the Bou Tchrafine and at the Jebel Ouaoufilal were studied by MASSA (1965), HOLLARD (1974), BULTYNCK & HOLLARD (1980), BENSAID et al. (1985), BECKER & HOUSE (1994), and others. The three late Emsian and Eifelian sections at the Jebel Ouaoufilal have not been previously published in detail (Text-Figs. 3,4,6,7).

The aims of this study are

1) to obtain information about the habitats of the two most important groups of late Emsian and Eifelian ammonoids, the Agoniatitina and Anarcestina,
2) to understand the relationship between sea-level fluctuations and conch parameters, and
3) to contribute data about gigantism in Emsian and Eifelian ammonoids.

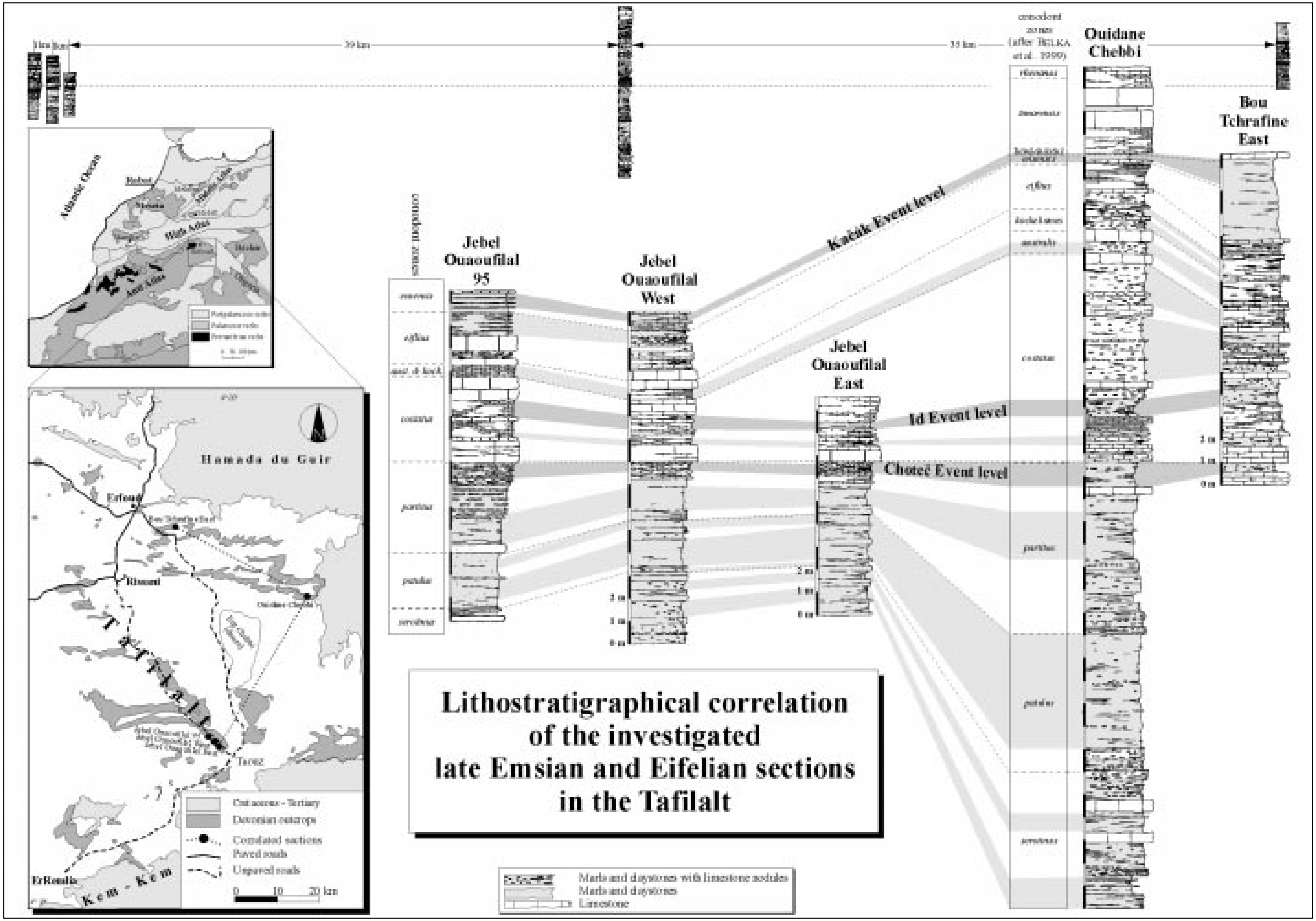
2. Localities, Material and Methods

2.1. Localities

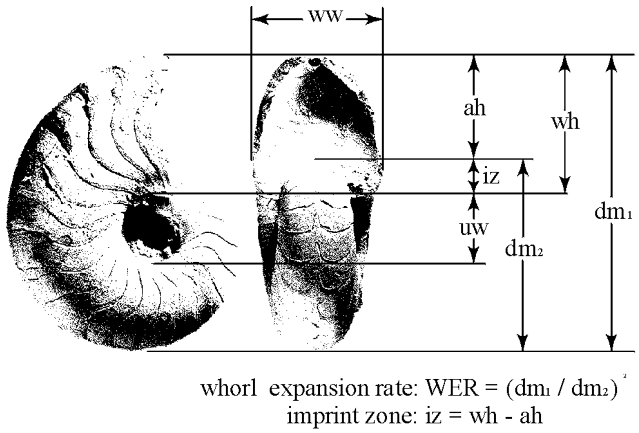
For the present study, five highly fossiliferous and well exposed sections in the Tafilalt were examined (Text-Figs. 1,3–9) and studied in detail. Access to these sections is possible by using the only partially paved road from Erfoud to Taouz (via Merzouga). Eight kilometres after passing the Ziz valley, an unpaved road runs East, just North of the Bou Tchrafine ridge. After six kilometres on this dirt road, the section Bou Tchrafine East can be seen directly south of the road. Ouidane Chebbi can be reached by continuing on the paved road and later following the largest unpaved road towards the dunes. Directly south of the oasis of Derkaoua, a dirt road turns east towards the high plateau of the Hamada du Guir (Algeria). After about 10 km, the erosional remnant of Cretaceous rocks in Ouidane Chebbi (about 30 km from Derkaoua) becomes visible and can be used for orientation. Just north-east of this mountain, the locality Ouidane Chebbi is located. The sections at the Jebel Ouaoufilal can be reached from Taouz, where a dirt road turns north-west across the Oued Ziz. The localities are positioned south-west of the Jebel Ouaoufilal (an erosional remnant consisting of late Famennian to Tournaisian sandstones) which can be seen from Taouz.

2.2. Material

The entire material is deposited in the Institut und Museum für Geologie und Paläontologie in Tübingen (Germany) with the numbers GPIT 1849-159 to -310 (Ouidane Chebbi) and 1862-1 to -397 (Jebel Ouaoufilal and Bou Tchrafine East). Most of the about 500 ammonoid specimens are preserved as limestone steinkerns, some with remains of the calcitic shells. Within these late Emsian and Eifelian sections, only a few horizons with haematitized ammonoid steinkerns occurs. In Ouidane Chebbi and in Bou Tchrafine East, such a fauna from the Kačak Event-level was assembled (similar haematitized faunas occur in the entire northern Tafilalt). Additionally, Thomas BECKER (Berlin, pers. comm.) reported a haematitized ammonoid assemblage from the Chotec Event level in the northern Tafilalt.



Text-Fig. 1.
Geological map of the eastern Anti-Atlas showing the localities and sections with the correlation of the five lithological columns.
Grey shaded areas correlate lithological units which were deposited at a relatively high sea-level. Map modified after S. Döring & M. Kazmierczak, (Tübingen).



Text-Fig. 2.
Descriptive terms of the conch and ornament features are adopted from KORN (1988, 1997).
dm = conch diameter; ww = whorl width; wh = whorl height; uw = umbilical width; ah = apertural height.

2.3. Conch Parameters

2.3.1. Maximum Conch Diameter

Many biological and sedimentological processes affect the pattern of conch diameter variation (BAYER & MCGHEE, 1985; BATT, 1989; BECKER, 1996a,b; NEIGE et al., 1997; WIESE, 1999). Sorting, transport of the dead animal, reworking, and corrosion can alter the recorded conch diameter. However, the variation of this parameter through time shows a close relationship to ecological changes, especially larger turnovers such as global eustatic events.

Small average conch diameters of ammonoid assemblages can be caused by sedimentological (sorting, fragmentation) or biological processes (paedomorphosis, mass-mortality of juveniles due to R-strategy, or environmental conditions). Clarity of both the systematics and the growth stage of the individuals is needed to determine the causes. The same applies to gigantism which is discussed in detail in chapter 4.

The maximal conch diameters were evaluated by counting samples which are either dominated by rather large or small specimens and correlated to the relative sea-level (Text-Fig. 14).

2.3.2. Whorl Expansion Rate

One important conch parameter is the whorl expansion rate (WER, Text-Fig. 2). It can be calculated by the algorithm used by RAUP & MICHELSON (1965), or in the simplified form as proposed by KORN (2000).

RAUP & MICHELSON:

$$WER = (r_1/r_2)^2$$

r_1 = radius from the centre of the protoconch to the venter at the aperture; r_2 = radius from the centre of the proto conch to the venter 180° behind the aperture.

KORN:

$$WER = [dm/(dm–ah)]^2$$

or

$$WER = [dm_1/dm_2]^2$$
$$\text{with } dm_1 = dm_2 + ah$$

dm_1 = maximal conch diameter; dm_2 = conch diameter 180° behind the aperture where dm_1 was measured; ah = apertural height.

Both methods yield consistent results when the coiling of the ammonoid conch is an exact logarithmic spiral. Minor differences occur when the ontogenetic development of the conch shows irregularities such as allometric growth or, as seen in the Agoniatitina, when distinct growth stages display a significant opening (and subsequent closing) of the aperture. The much easier and more precise applicability of the new method, however, justifies its use.

Major differences in the measurement of the whorl expansion rate occur in gyroconic and advolute ammonoids. Using the method of RAUP & MICHELSON (1965), the gyroconic *Anetoceras* would display a very high whorl expansion rate, whereas the advolute whorls of *Erbenoceras* (with the whorls touching each other) have very small values. It is clear that both genera are closely related (ERBEN, 1964), and that the major arithmetic discrepancy between the two genera does not show their true phylogenetic (and probably also ecological) distance. The new method probably reflects the growth of the soft body during ontogeny more precisely.

Calculation of the whorl expansion rates is an easy method to estimate the length of the body chamber. Brevidomic ammonoids have high whorl expansion rates whereas longidomic forms have slowly expanding whorls. This becomes biologically relevant because it affects the life position of the aperture (SAUNDERS & SHAPIRO, 1986; WESTERMANN, 1996). WESTERMANN & TSUJITA (1999) suggest a rather stable position of ammonoids with brevidomic conchs (living chamber ½ whorl, high WER) with a good manoeuvrability on the one hand and a comparatively unstable position in ammonoids with longidomic conchs (living chamber about one whorl, low WER) on the other hand with a planktonic lifestyle ("passive floaters").

The value of the whorl expansion rate allows a subdivision of ammonoid coiling:

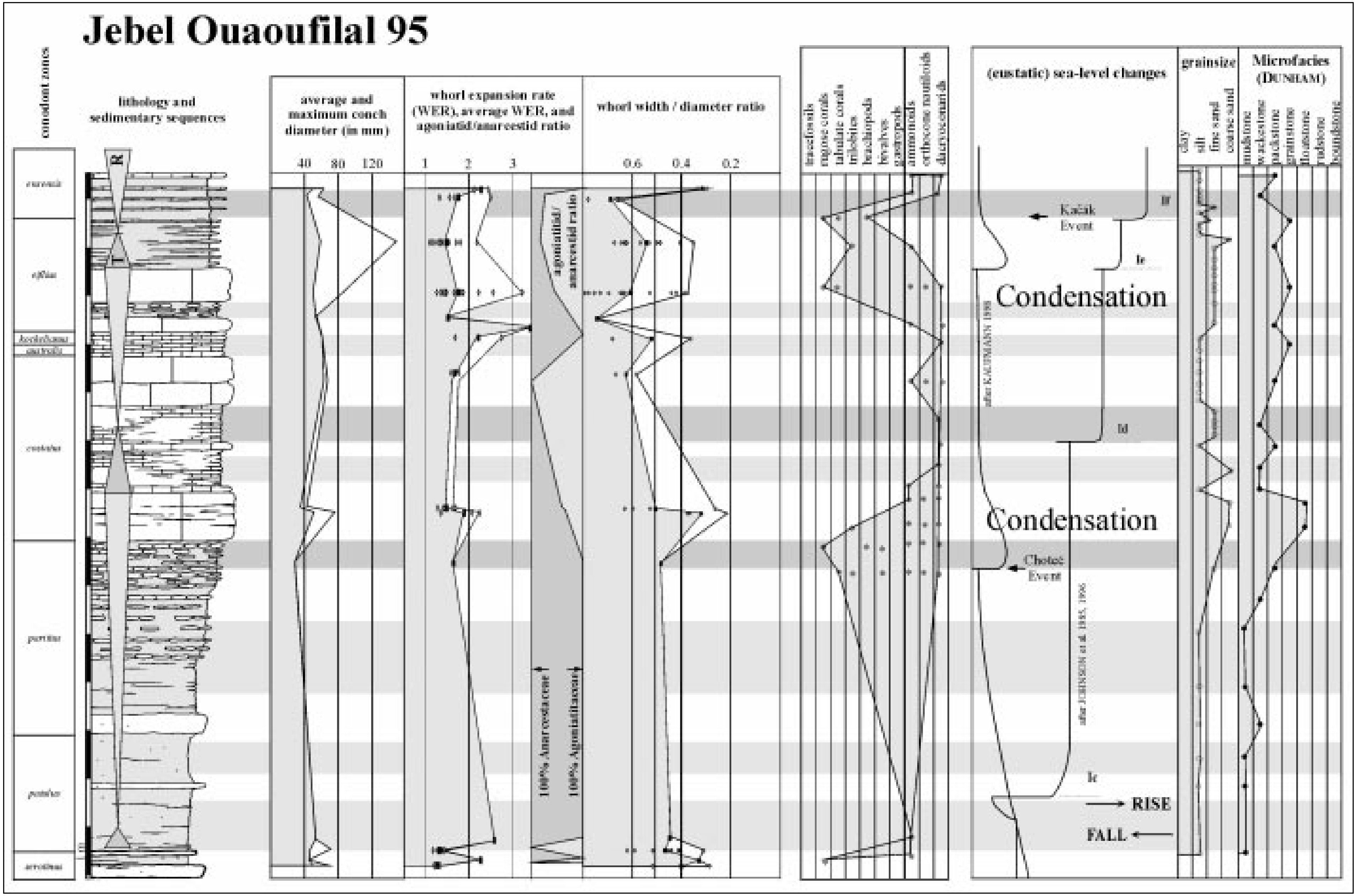
– low (WER <1.60);
– moderate (WER = 1.61–2.00);
– moderately high (WER = 2.01–2.40);
– high (WER = 2.41–2.80);
– very high (WER >2.81).

Most Emsian and Eifelian ammonoids belong to the suborders Agoniatitina and Anarcestina. They can easily be distinguished by their whorl expansion rates: Most adult representatives of the Agoniatitina have WER values of over 2.2, where as the Anarcestina values are mostly below 2.0 (Text-Fig. 10).

2.3.3. Whorl Width/Conch Diameter Ratio

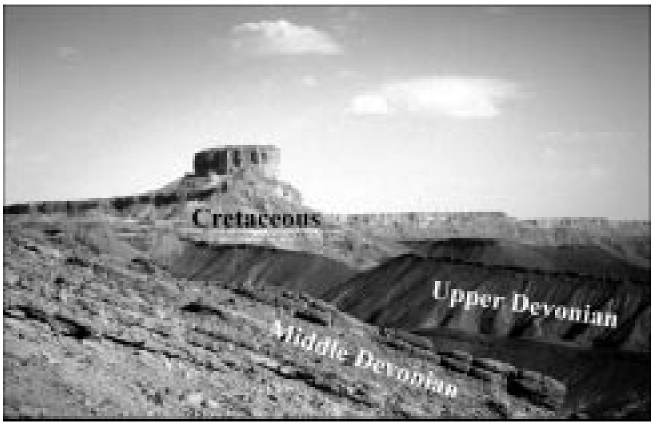
RAUP (1967) used the whorl width to define the shape of the generating curve S. S equals the ratio of the whorl width and the whorl height. For this study, the whorl width/conch diameter ratio was preferred, because it reflects the flow resistance of the ammonoid conch. With increasing whorl width/conch diameter ratio the flow resistance increases (i.e. the drag coefficient: JACOBS [1992]; TSUJITA & WESTERMANN, [1998]). However, whether currents or wave action affected the ammonoid habitat can only be decided from sedimentological features (chapter 2.5.; wave ripples, tool marks, tempestites, current-aligned shells, etc.) and from the associated organisms (chapter 2.4.).

The whorl expansion rates of all ammonoid specimens were plotted versus the whorl width/conch diameter ratio (Text-Fig. 10). It turned out that the adult conchs of Emsian and Eifelian Agoniatitina and Anarcestina occupied two clearly separated morpho-



Text-Fig. 3.
Section Jebel Ouaoufilal 95 with conch parameter curves, accompanying fauna, and sedimentological parameters.
Each single black or white bar equals 1 m.

Text-Fig. 4.
Section Jebel Ouaoufilal West with the Eifelian limestones forming the crest and the Emsian claystones, marls and limestones in the slopes.



Text-Fig. 5.
Section Ouidane Chebbi with the Eifelian and Givetian limestones forming the crest and the dark grey claystones, marls and limestones of the Late Devonian in the slopes of the following crest.
The Paleozoic rocks are discordantly overlain by Cretaceous sandstones and limestones of the Hamada du Guir.

spaces. Only preadult specimens of both taxa display an overlap in the whorl expansion rate values. Furthermore, most anarcestids have higher whorl width/conch diameter ratios (0.4 to 0.9) and thus a higher drag coefficient. This might indicate a poor adaptation to high energy environments. In contrast, the agoniatids had less diverse and smaller whorl width/conch diameter ratios ($<$0.6). Their conchs were more slender and possibly better adapted for shallow water environments with comparatively strong water movements (wave action, currents).

2.4. Associated Organisms

Accompanying faunas of each ammonoid sample were documented and plotted separating two groups: benthic organisms (gastropods, bivalves, trilobites, rugose and tabulate corals) and trace fossils on the left side, and the nektonic and planktonic faunal elements (ammonoids, nautiloids, dacryoconarids; Text-Figs. 3,6–9) on the right side. Absence of representatives of the benthic organisms in many samples might indicate episodic hypoxic bottom waters. Crinoid remains were ignored, because their disarticulated sclerites are lighter than water prior to cementation (RUHRMANN, 1968) and hence are almost equally distributed throughout the sections.

Remains of non-animal organisms are very rare in the five sections. However, some shell fragments encrusted by cyanobacteria were discovered in the sediments of the earliest *eiflius* Zone in the Jebel Ouaoufilal 95 section. From these findings, a shallow sea-level with a sunlit sea-floor in this region can be concluded. Additionally, multioculated trilobites are abundant in some horizons which were deposited under shallow marine conditions.

2.5. Sedimentological Parameters

The microfacies (terminology after DUNHAM) was first defined in the field and later, numerous thin sections were studied to confirm the field results. Simultaneously, the average grainsize (Text-Figs. 3, 6–9) was estimated. Certainly, both parameters reflect the energy-level within the depositional system and the bathymetry.

The sea-level curves were obtained from JOHNSON et al. (1985, 1996) and KAUFMANN (1998). They were correlated with the sections based on conodont stratigraphy and lithology. Additionally, local or less significant sea-level high-stands are indicated in the Text-Figs. 3,6–9 as grey rectangles under the graphs with the conch and the sedimentological parameters.

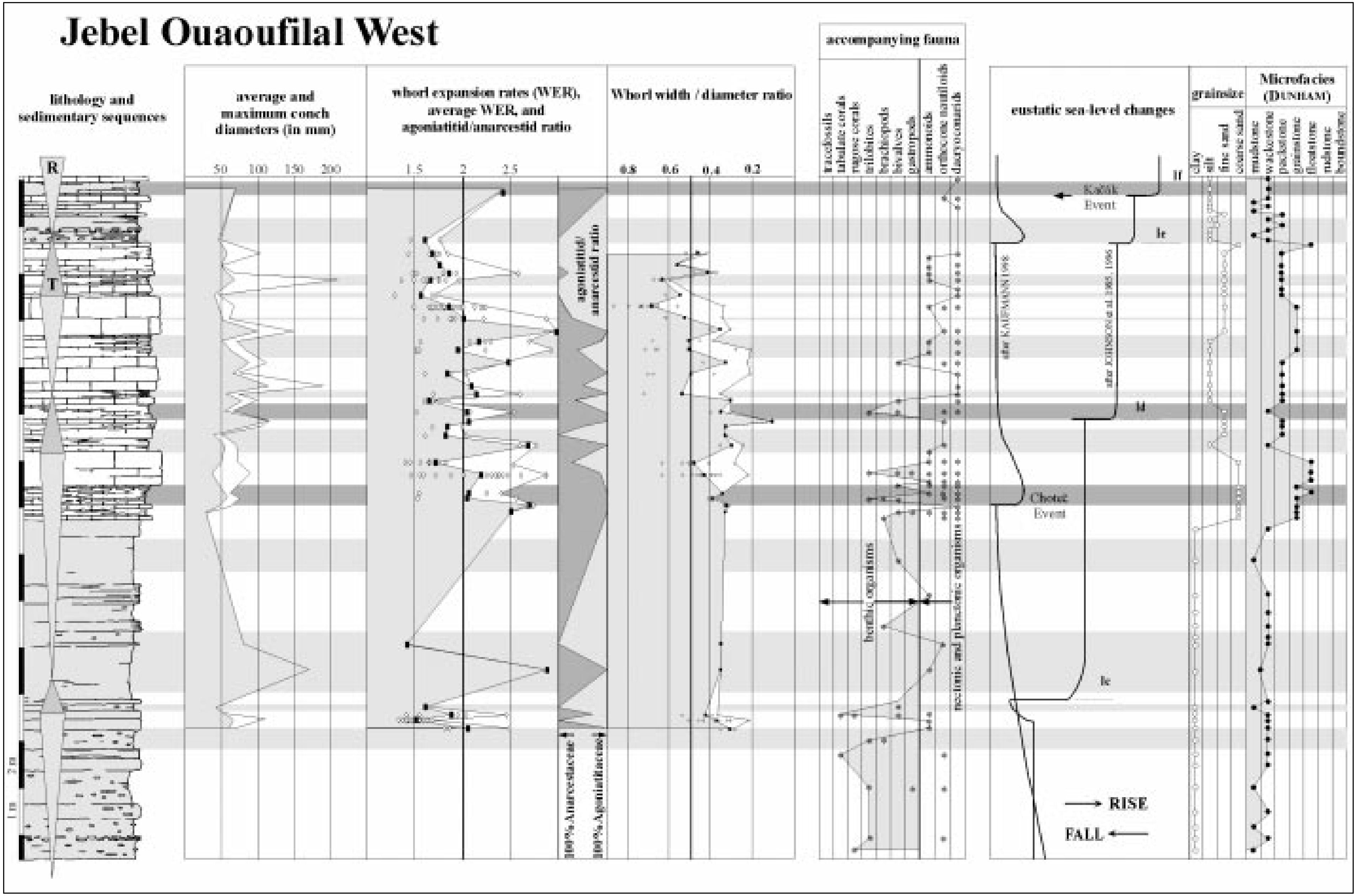
3. Stratigraphy, Global Events, and Ammonoid Associations

In the Tafilalt, the thickness of Emsian sedimentary rocks measures about 50 metres south of Taouz up to over 200 m at the Jebel Mech Agrou. The Eifelian deposits are 7 m thick at El Atrous, approximately 100 m between the Jebel Amessoui and Tizi Nersas, and about 230 m at the Irhfelt n'Tissalt (KAUFMANN, 1998). These values reflect a complex pattern of basins with monotonous, sometimes laminated mudstones and submarine rises with condensed facies consisting of cephalopod limestones and marls ("Schwellen" [WENDT, 1985, 1988; WENDT & AIGNER, 1984]).

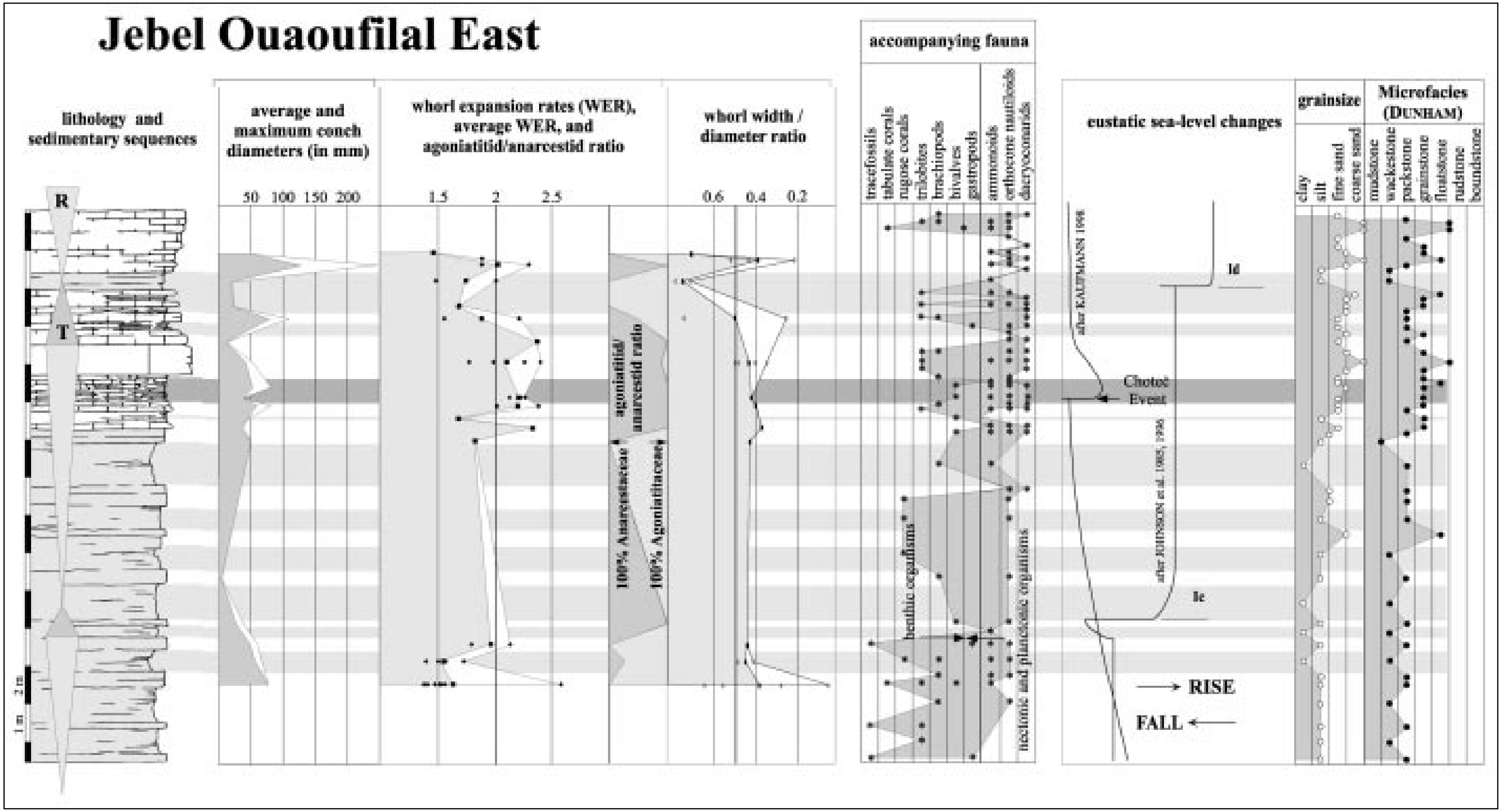
The studied succession belongs to the Amerboh Group and the lower Bou Tchrafine Group. In the Ma'der, the equivalent of the Amerboh Group is the ErRemlia Formation (late Emsian) and the Tazoulait Formation (latest Emsian). Early and middle Eifelian deposits in the Ma'der were named El Otfal Formation (lower Bou Tchrafine Group in the Tafilalt) and the late Eifelian lower Buttes de Taboumakhlouf Formation can be correlated with the upper Bou Tchrafine Group (HOLLARD, 1974, 1981). The succession of the ammonoid-bearing strata under consideration is as follows (conodont zones in bold type, Text-Figs. 3,6–9):

Daleje Event
Early ***inversus*** Zone, late Emsian

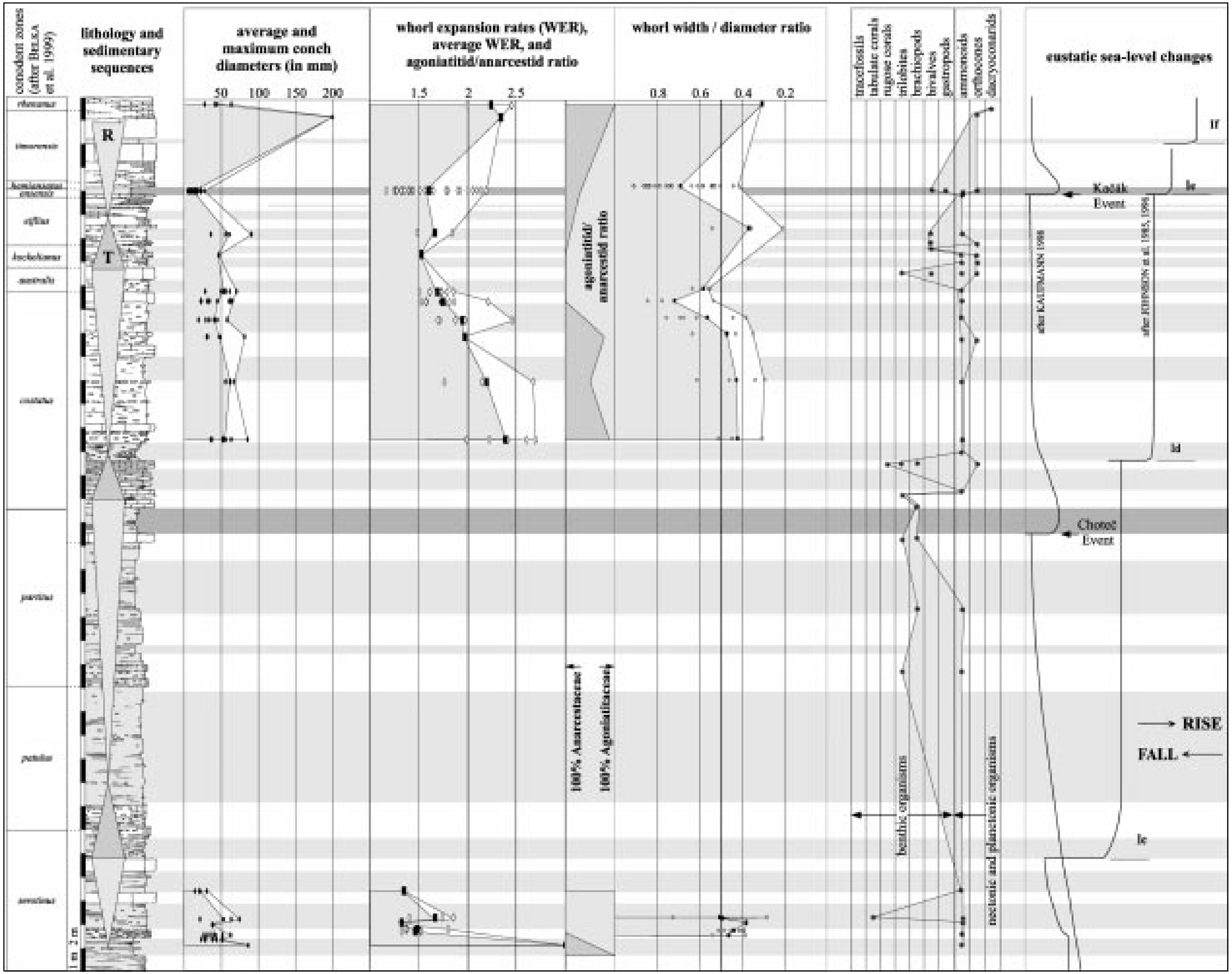
In the eastern Anti-Atlas, the Daleje Event level is marked by a sharp lithologic change from fossiliferous thick-bedded limestones with *Mimagoniatites fecundus* (BARRANDE 1865) to greenish/greyish claystones with a significantly lower fossil content (MASSA, 1965; HOLLARD, 1974; KAUFMANN, 1998; BELKA et al., 1999). CHLUPÁČ & KUKAL (1986) were the first to recognize the importance of this level. It can be correlated with the younger of the two intra-Ib transgressions (JOHNSON et al., 1985, 1996). The rare haematitized fossils of benthic organisms (gastropods, brachiopods, trilobites) indicate a poorly oxygenated sea-floor. Some horizons within these claystones yield small haematitized specimens of *Gyroceratites*, *Mimagoniatites*, *Latanarcestes*, and *Praewerneroceras*. Among these genera, those with high whorl expansion rates are remarkably rare (i.e. *Mimagoniatites*). This horizon can be interpreted as the base



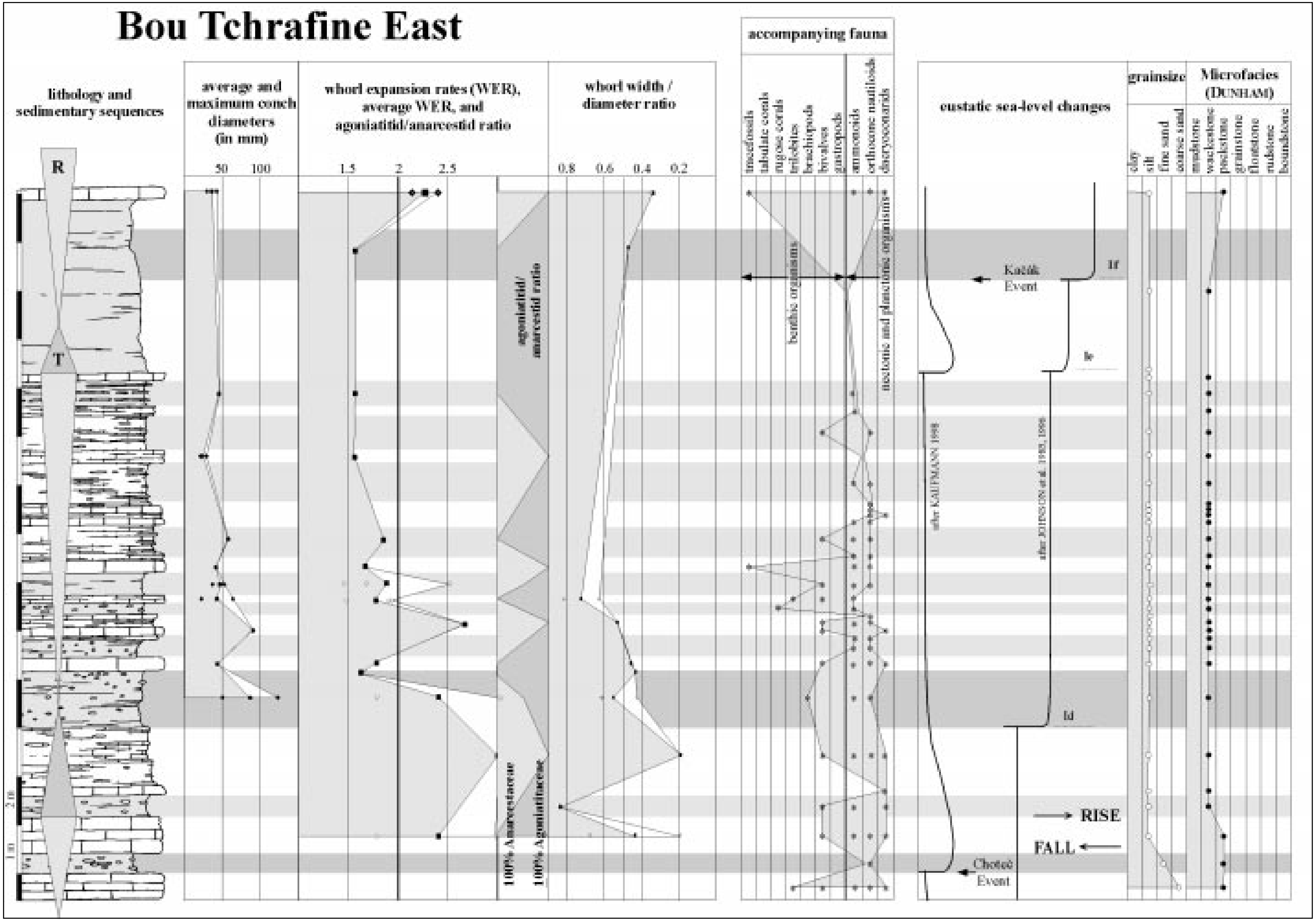
Text-Fig. 6.
Section Jebel Ouaoufilal West with conch parameter curves, accompanying fauna, and sedimentological parameters.
Each single black or white bar equals 1 m.



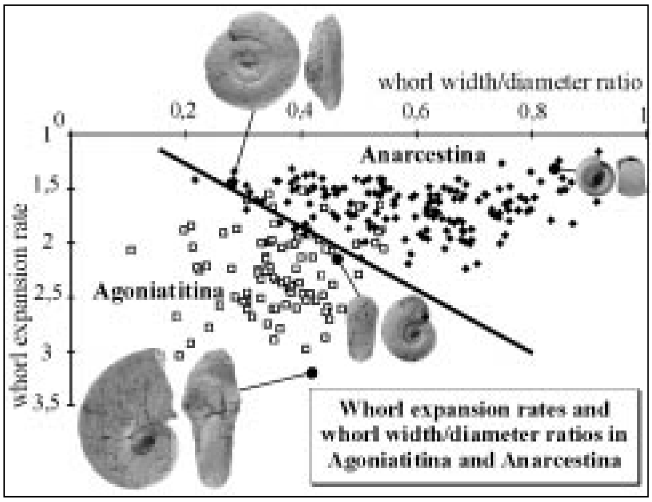
Text-Fig. 7.
Section Jebel Ouaoufilal East with conch parameter curves, accompanying fauna, and sedimentological parameters.
Each single black or white bar equals 1 m.



Text-Fig. 8.
Section Ouidane Chebbi with conch parameter curves, accompanying fauna, and sedimentological parameters.
Each single black or white bar equals 1 m.



Text-Fig. 9.
Section Bou Tchrafine East with conch parameter curves, accompanying fauna, and sedimentological parameters.
Each single black or white bar equals 1 m.



Text-Fig. 10.
Whorl expansion rates and whorl width/diameter ratios of the Agoniatitina (white square) and Anarcestina (black rhombus).
Note the separate areas occupied by the two taxa: Anarcestina have whorl expansion rates below 2, but the ww/dm ratio varies considerably. Most of the representatives of the Agoniatitina in the overlapping field are preadult specimen.

of a large scale thickening and shallowing upward sequence which terminates in the Givetian.

Towards the top of the late Emsian claystones, the carbonate content increases and the intercalated marly nodules and nodular limestone horizons become more densely spaced. Based on lithology (increasing carbonate content), faunal associations (growing number of benthic organisms), and microfacies (change from mudstones to wacke- and packstones), this interval is interpreted as the top of a medium scale thickening upward and also shallowing upward sequence. In the nodular limestones of the early *Anarcestes lateseptatus* Fauna (*serotinus* Zone), the genera *Sellanarcestes*, *Anarcestes*, and *Latanarcestes* occur quite frequently, whereas representatives of *Mimagoniatites*, *Paraphyllites*, *Amoenophyllites*, and *Chlupacites* are comparatively rare. One feature of the ammonoid distribution in this unit is repeated in the pattern that also can be recognized in the Eifelian rocks: all ammonoid bearing layers contain either agoniatids or anarcestids, and consequently, the conch parameters parallel this pattern. The ammonoids are associated with trilobites, tabulate corals, bivalves, crinoids, orthocone nautiloids, etc.

In the claystones, marls, and nodular limestones of the late *Anarcestes lateseptatus* Fauna (*patulus* Zone), ammonoid records are very rare. The oldest representatives of the ammonoid taxa *Fidelites* and *Foordites* were found just below the first more massive and less marly nodular wackestone and packstone layers of early Eifelian age.

Chotec Event
Pinacites jugleri Fauna, *partitus* Zone, early Eifelian

In Bohemia (CHLUPÁČ, 1985), Germany (REQUADT & WEDDIGE, 1978), and northern Spain (HENN, 1985), the lithology in the Choteč Event level is characterised by dark grey dacryoconarid packstone to grainstone nodules embedded in dark grey claystones and marls. The same can be seen in many sections in the Tafilalt (ALBERTI, 1980; BECKER & HOUSE, 1994; KAUFMANN, 1998). Apparently, the event happened in the *partitus* Zone below the entry of *Pinacites jugleri*. For this reason, it was named the "*jugleri* Event" by WALLISER (1985). Benthic organisms play only a subordinate role, indicating poorly oxygenated bottom waters. However, findings of lingulid brachiopods in life position in probably the same level at the Jebel El Maharch (southeastern Ma'der) rather indicate oxic conditions.

Fidelites fidelis, Foordites sp. and *Pinacites jugleri* are the most abundant ammonoids in this level. Additionally, *Mithraxites* and *Subanarcestes* were recorded from this level but are rare. From the above, it can be concluded that the Agoniatitina dominate this level but the conch size curve displays a minimum in some of the studied sections (Text-Figs. 3,6–9).

Directly above this stratigraphical segment, one or two thick fossiliferous packstone to floatstone beds which sometimes are amalgamated occur in most sections of the Tafilalt (*Pinacites jugleri* Fauna, earliest *costatus* Zone). These beds are easily recognized because they contain numerous ammonoids, often in distinct levels within the beds. Besides iron-rich bands, the fossil content and the sometimes winnowed micritic matrix indicate condensed sedimentation and a relatively shallow sea-level. For these reasons, this horizon is interpreted as the top of a medium scale thickening upward and shallowing upward sequence.

Well preserved ammonoids and bactritoids with calcitic shell of all growth stages including ammonitellas and bactritellas are common in the three sections of the Jebel Ouaoufilal. This indicates reproduction of these cephalopods in this region. Some levels in this layer contain mainly *Fidelites* and *Pinacites* whereas others are dominated by *Subanarcestes* and *Werneroceras*. Both the whorl expansion rates and the conch diameters display fluctuations within this particular bed. The benthic fauna consists of gastropods, trilobites, rare rugose and tabulate corals, and bivalves.

In the subsequent lithological unit, the carbonate content of the nodular wackestones and packstones decreases and the claystone intercalations increase in thickness. Ammonoids are rare and the faunas mainly consist of representatives of *Fidelites*, *Pinacites*, rare *Werneroceras*, and one *Sellanarcestes* (?). Both conch diameters and whorl expansion rates display intermediate average values.

Transgression Id
Subanarcestes macrocephalus
to *Cabrieroceras plebeiforme* Fauna,
late *costatus* to early *australis* Zone, middle Eifelian

This short claystone interval can probably be correlated with the Id transgression (JOHNSON et al., 1985, 1996). Both from the conodont findings (indicating a stratigraphical position near the *costatus* Zone – *australis* Zone boundary) and the ammonoid findings (first occurrence of *Cabrieroceras*) a stratigraphical position as that described by JOHNSON et al. (1985, 1996) can be inferred. In many sections in the Tafilalt and in the Ma'der (pers. comm. M. KAZMIERCZAK, Tübingen), a lithological change to claystones in this interval can be studied. Representatives of *Fidelites*, *Pinacites*, *Werneroceras*, *Subanarcestes*, and *Cabrieroceras* occur in moderate numbers within these levels. In the middle Eifelian sediments (late *costatus* to early *australis* Zone), the whorl expansion rates and conch diameters of the ammonoids fluctuate strongly and rapidly. Sometimes, the variation of these conch parameters in subsequent layers is extreme (Text-Figs. 6,7).

The overlying sediments have a higher carbonate content and consist of nodular to massive wacke- and packstones (late *Cabrieroceras plebeiforme* Fauna, *australis* to early *kockelianus* Zone). The ammonoid fauna displays some remarkable features: "Giants" both of *Fidelites* sp. (with strong constrictions behind the aperture at diameters larger than 100 mm) and of *Exopinacites singularis* (with more than 200 mm in diameter) were discovered within this interval, accompanied by numerous specimens of *Werneroceras*, *Subanarcestes*, and *Cabrieroceras*. Average whorl expansion rates as well as conch diameters vary considerably in this unit. Predominantly nektonic and planktonic faunal elements are associated with the ammonoids in this unit. In two sections at the Jebel Ouaoufilal, shell-fragments encrusted by cyanobacteria were found near the top of this interval indicating shallow water conditions. As for the early *costatus* Zone limestones, the top of this unit is interpreted as the top of a medium scale thickening upward and shallowing upward sequence.

Transgression Ie
Agoniatites vanuxemi Fauna
kockelianus Zone, late Eifelian

This global transgression in the late Eifelian is often difficult to recognize. In most sections, the lithology of this unit persists into the Kačák Event-level. Moreover, the exact biostratigraphic assignment of this level often remains unclear, because either the ammonoids were surface collected or this unit is covered by talus deposits.

Kačák Event
Transgression If
Agoniatites vanuxemi Fauna
ensensis Zone, late Eifelian

Many of the late Eifelian sections in the Tafilalt show that the carbonate content decreases considerably (MASSA, 1965) and this claystone interval is only interrupted by some layers of nodular dacryoconarid wackestones. Various names have been assigned to this interval: "otomari" and "rouvillei" (HOUSE, 1985; WALLISER, 1985); "Great Gap", "Late Eifelian Events 1 + 2", "Odershausen Events" (BECKER et al., in WEDDIGE, 1996). The accompanying benthic fauna is sparse: Only few specimens of gastropods and bivalves were collected with the ammonoids.

Remarkably, giant *Cabrieroceras crispiforme* specimens (dm >150 mm, Text-Fig. 11) occur in one of the more massive limestone beds in this unit. Besides this taxon, representatives of *Subanarcestes*, *Parodiceras*, and *Werneroceras* are common. At Bou Tchrafine and Ouidane Chebbi, this interval yields mainly small haematitized specimens of *Agoniatites*, *Cabrieroceras*, *Subanarcestes*, *Werneroceras*, *Parodiceras* and *Sobolewia*. In Ouidane Chebbi and at the Jebel Ouaoufilal, the top of this unit can be correlated with the Kačák Event level based on the facies, conodonts (*ensensis* Zone), and ammonoids (haematitised fauna in the northern Tafilalt). In all sections however, the average conch diameters and whorl expansion rates of the ammonoids are small in the Kačák Event-level. With the features discussed above, this hypoxic event-level can be interpreted as the base of a medium scale thickening upward and shallowing upward sequence.

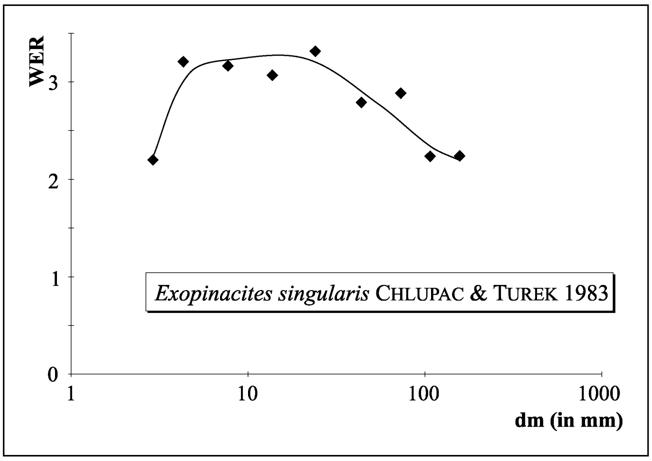
In the sections of Bou Tchrafine and Ouidane Chebbi, the Kačák Event-level is followed by thick and massive limestone layers with trace fossils and abundant large *Agoniatites* specimens (dm >100 mm). This unit was dated as early Givetian (*Maenioceras undulatum* Fauna, *hemiansatus* to *timorensis* Zone). Low ammonoid diversity, large conch diameters, high whorl expansion rates, and a sparse accompanying fauna are characteristic of these beds. In the Jebel Ouaoufilal sections, allochthonous deposits with large colonies of stromatoporoids, rugose and tabulate corals occur (probably debris-flow deposits). These faunal and sedimentological features indicate that this unit represents the top of another medium scale thickening upward and shallowing upward sequence.

4. Gigantism in Early and Middle Devonian Ammonoids

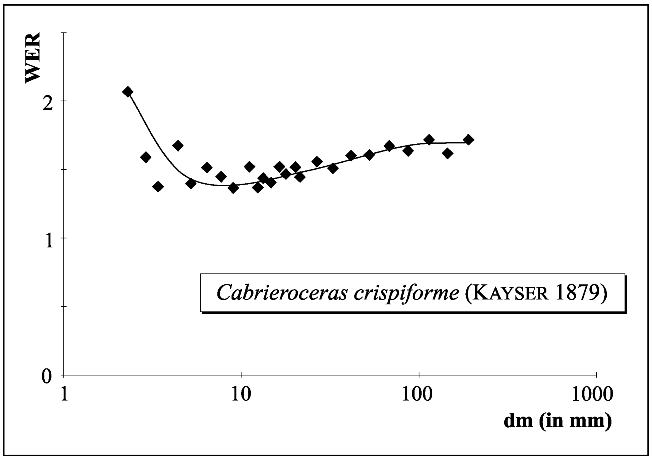
LANDOIS (1895) was the first to publish giant specimens of *Parapuzosia seppenradensis* from the early Campanian of Seppenrade in the northwest of Germany. More recently, STEVENS (1988) compared recent giant squids (*Architeuthis*) with Mesozoic giant ammonoids.

He concluded that large ammonoids lived in the deep sea and migrated into more shallow shelf habitats with rising sea-levels. MANGER et al. (1999) described two types of gigantism in molluscs. "Phyletic gigantism" includes all giant forms which normally attain large adult sizes (such as the giant squid *Architheuthis*). "Pathological gigantism" was reported only from recent gastropods, in which it is caused by infestation of nematodes leading to castration. For the giant Pennsylvanian cephalopods of the southern Midcontinent of America, MANGER et al. (1999) suggested pathological gigantism. According to him, "the cephalopod assemblages reflect mass mortality of mature individuals probably as a consequence of reproduction (semelparity)". None of his giant ammonoids shows indicators for sexual maturity (septal and growth line crowding, mature modifications, change in ornament). He concluded that for probable pathological reasons these "giants" did not achieve sexual maturity and continued to grow to large sizes.

Text-Fig. 11.
Mould of a giant specimen of *Cabrieroceras* sp. (reconstructed diameter about 250 mm) with phacopid trilobite in the living chamber from the late Eifelian (*ensensis* Zone) of the section Jebel Ouaoufilal 95.



Text-Fig. 12.
Whorl expansion rates through ontogeny in *Exopinacites singularis* CHLUPÁČ & TUREK 1983.
kockelianus Zone, late Eifelian, Jebel Ouaoufilal East.



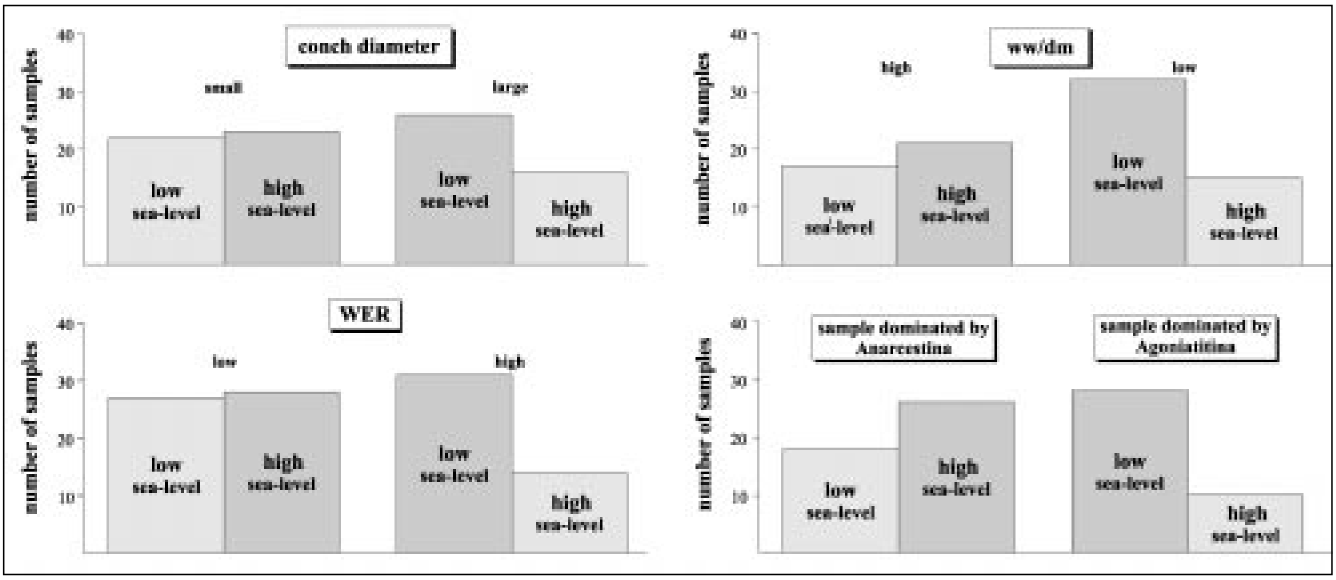
Text-Fig. 13.
Whorl expansion rates through ontogeny in *Cabrieroceras crispiforme* (KAYSER 1879).
kockelianus Zone, late Eifelian, Jebel Ouaoufilal East.

Representatively, the two largest Emsian and Eifelian ammonoid specimens available for this study from Morocco were measured. In the whorl expansion rate/diameter and whorl width/diameter graphs, slight changes in the growth can be seen. The slow decrease in the whorl expansion rate of large *Exopinacites singularis* (dm = 235 mm) is a characteristic of adult agoniatids (Text-Fig. 12). However, this species has a rather large average conch diameter (dm = 130 mm). The stable whorl expansion rate during most of their ontogeny is typical for the anarcestids (Text-Fig. 13). In *Cabrieroceras crispiforme*, the average conch diameter is moderate (dm = 49 mm) whereas the “giant” measures 190 mm in diameter. Unfortunately, no traces of septa are preserved in the two specimens, and hence, evidence for septal crowding is lacking. A slight increase in the whorl expansion rates of such large specimens might indicate adulthood. The discrepancy from the number of such “giant” and “adult” *Cabrieroceras* to the significantly larger number of smaller specimens is remarkable. It should be noted, however: Most large ammonoid specimens from the Emsian and Eifelian were extracted from sediments which were deposited in rather shallow water. This is corroborated by the large *Cabrieroceras* specimen mentioned above which is encrusted by stromatolites.

5. Ammonoid Habitats in the Emsian and Eifelian of the Tafilalt

In the late Emsian and Eifelian, the alternating predominance of the Anarcestina versus the Agoniatitina is reflected in the ammonoid "zonation": *Sellanarcestes wenkenbachi (Anarcestina) – Anarcestes lateseptatus (Anarcestina) – Foordites platypleura (Agoniatitina) – Pinacites jugleri (Agoniatitina) – Subanarcestes macrocephalus (Anarcestina) – Cabrieroceras plebeiforme (Anarcestina) – Agoniatites vanuxemi (Agoniatitina)*.

Seeking an explanation for this pattern, the lithology of the sections was explained by sea-level changes and a coarse scheme of large and medium scale sedimentary sequences was superimposed (chapter 3.). After analysing the biometric and the sedimentological data, the correlation of these parameters were evaluated: The number



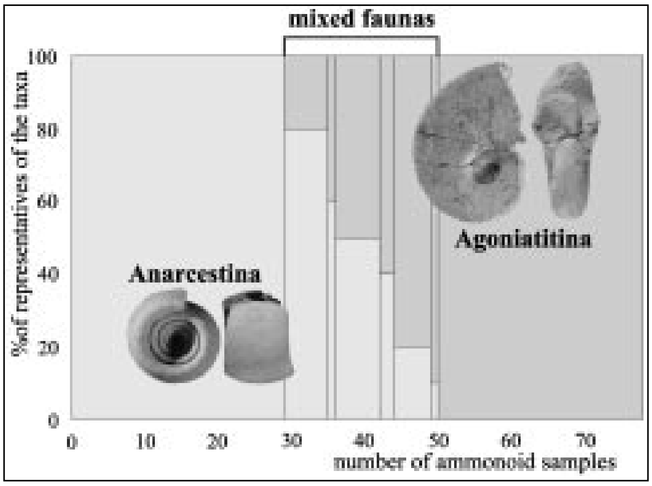
Text-Fig. 14.
Conch diameters, whorl expansion rates, whorl width/diameter ratios, and Agoniatitina/Anarcestina ratios of all ammonoid samples used in this study.
Number of ammonoid samples with low or high values of the conch parameters from high or low sea-level sediments. The dark grey shaded rectangles highlight the predominant correlation of these representative conch parameter-values with the high or low sea-level.

of ammonoid samples with high average WER which were extracted from sediments deposited under high sea-level were counted and vice versa (high WER: low sea-level; low WER: high sea-level; low WER: low sea-level). Accordingly, the samples with high average conch diameters from shallow water sediments were counted and vice versa (Text-Fig. 14).

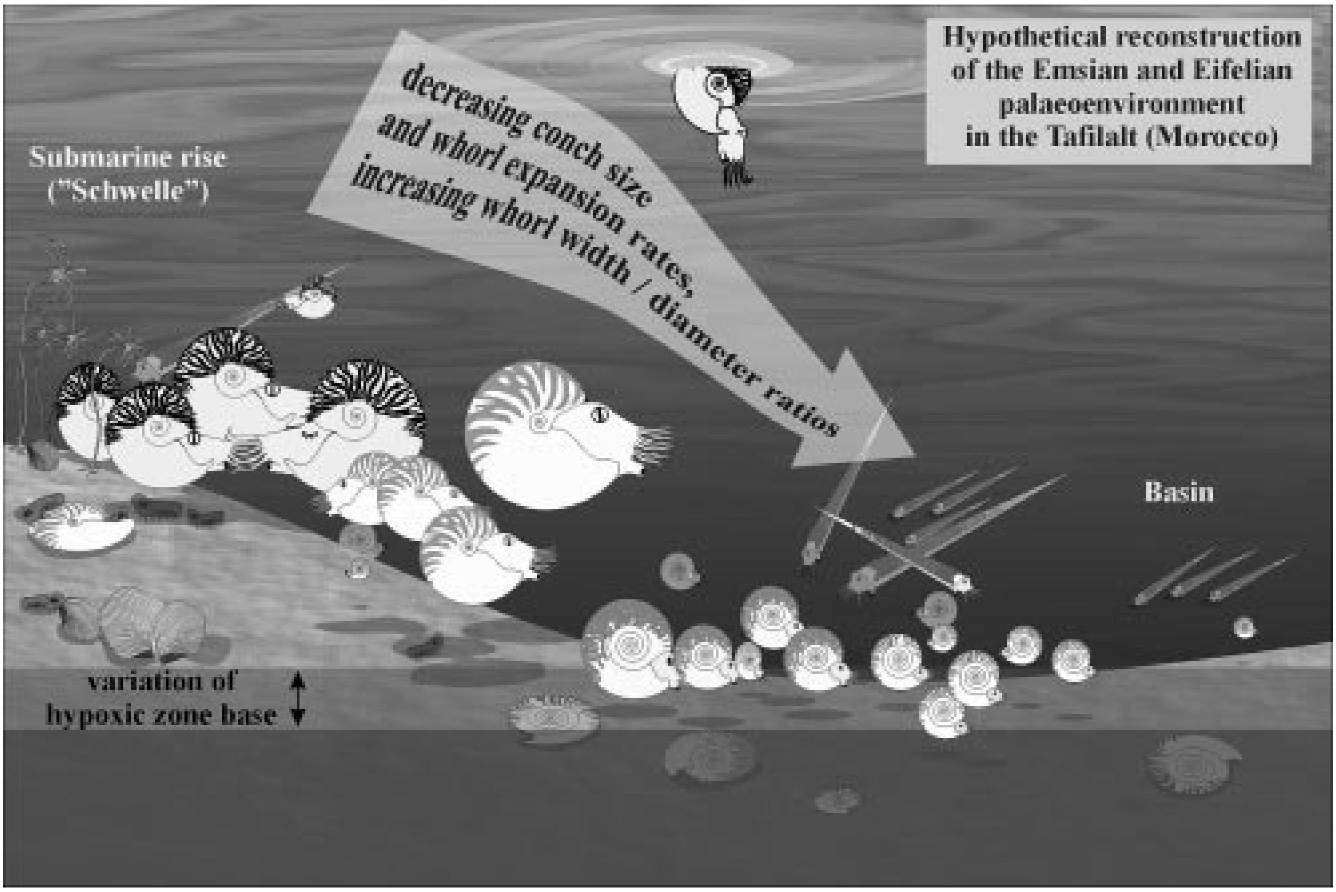
It turned out that almost 70 % of the samples with high average whorl expansion rates and large average conch diameters (including the "giants") were extracted from layers which were deposited in relatively shallow water. However, ca. 50 % of the samples containing ammonoids with low average whorl expansion rates and small average conch diameters were taken from sediments indicating deeper environments. This distribution can be explained by the change in whorl expansion rates during the ontogeny of the Agoniatitina. Preadult specimens belonging to this suborder have significantly lower whorl expansion rates than adults (Text-Figs. 10,12). Correlation of the Agoniatitina/Anarcestina ratio with the relative sea-level display a clearer picture with about 70 % of the samples dominated by the Agoniatitina originating from sediments with shallow water indicators.

From the data listed above, it can be concluded that most of the Emsian and Eifelian anarcestids which have small conch diameters and low whorl expansion rates lived in areas with comparatively deeper water or with anoxic to hypoxic conditions near the sea-floor (e.g. Choteč and Kačák Event levels). Ammonoids with large conch diameters and high whorl expansion rates (Agoniatitina) preferred areas with rather shallow water (Text-Fig. 16).

Mixed ammonoid faunas with approximately equal numbers of representatives of both the Anarcestina and the Agoniatitina are very rare: Of 78 ammonoid faunas collected in situ only 21 are mixed assemblages with representatives of both suborders, and in only nine cases the Agoniatitina/Anarcestina ratio approximates 50 % to 50 % (Text-Figs. 15,16). Rapid fluctuations in the conch parameters and synchronously in the Agoniatitina/Anarcestina ratio are interpreted as the result of migrations of populations of the two taxa following sea-level changes (compare Bayer & McGhee, 1985). Samples containing all growth stages of ammonoids indicate reproduction of the ammonoids within the study area. Therefore, repeated immigration of populations of either one of the taxa from distant regions and extinction is rather unlikely.



Text-Fig. 15.
Percentages of Agoniatitina and Anarcestina in the ammonoid samples.



Text-Fig. 16.
Hypothetical reconstruction of the habitats of Emsian and Eifelian ammonoids in Morocco.

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