



Morphometric Analyses and Taxonomy of Oxyconic Goniatites (Paratornoceratinae n. subfam.) from the Early Famennian of the Tafilalt (Anti-Atlas, Morocco)

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13 Text-Figures and 1 Table

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Morphometrische Analyse und Taxonomie oxyconer Goniatiten (Paratornoceratinae n. subfam.) aus dem unteren Famennium des Tafilalt (Anti-Atlas, Marokko)

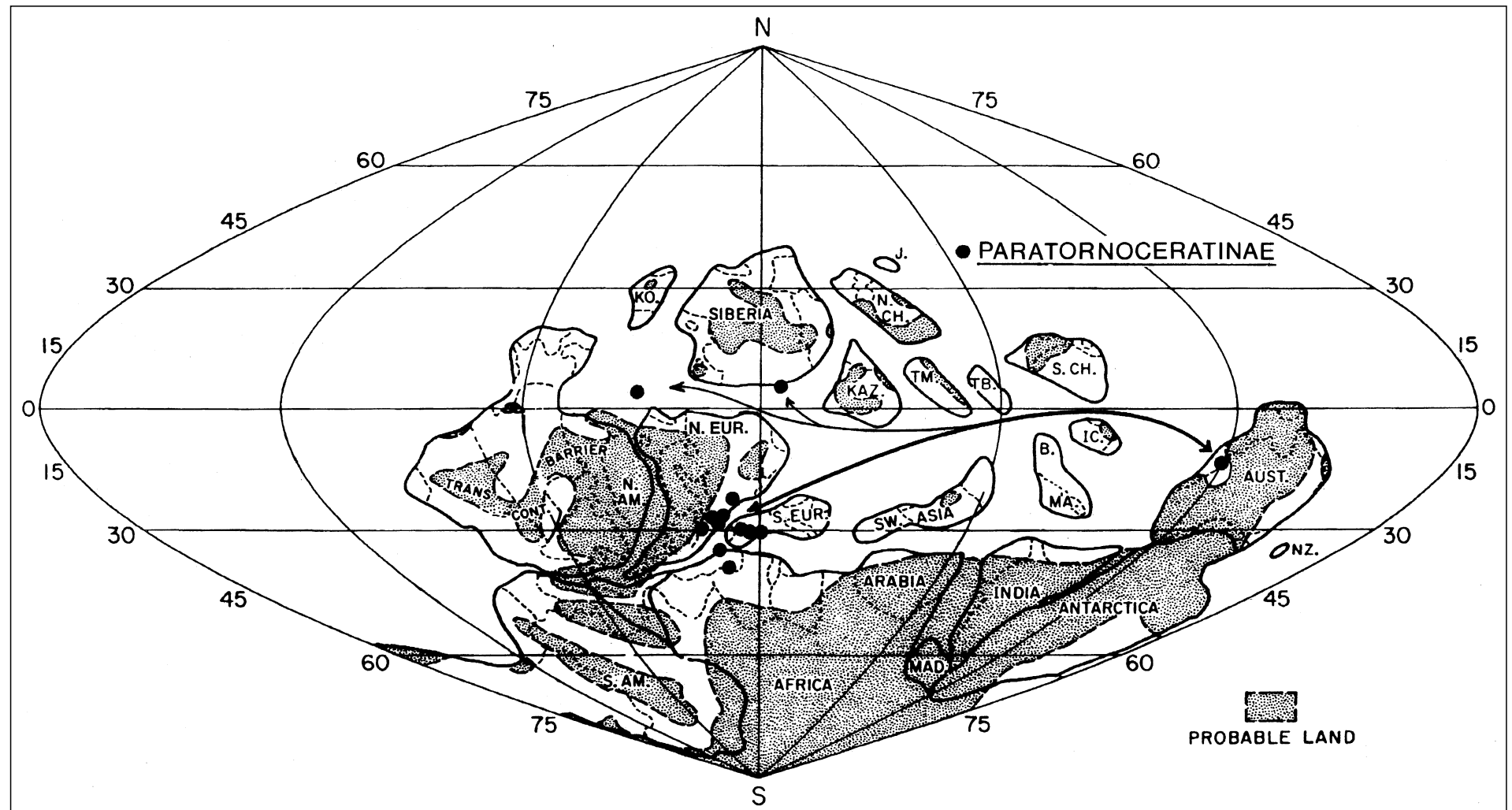
Zusammenfassung

Innerhalb der Dimeroceratidae (Goniatitida, Tornoceratina) werden Vertreter der oxyconen Entwicklungslinie in der neuen Unterfamilie Paratornoceratinae zusammengefasst, welche global in fast allen Gebieten mit reichen Ammonoideen-Faunen des höheren Oberdevon II (Nehden-Stufe, UD II-F/II-I) verbreitet war. Zwei systematisch ausgegrabene Populationen von Dar Kaoua im zentralen Tafilalt (östlicher Anti-Atlas, S-Marokko) werden morphometrisch analysiert, um exemplarisch Fragen der intraspezifischen Variabilität, möglicher Chronomorphoklinen und der Verbreitungsmuster einer nach bisherigen Vorstellungen artenarmen aber vielgestaltigen oxyconen Goniatiten-Gruppe zu klären. Es zeigte sich, dass es sich um zwei völlig getrennte Taxa handelt, *Acrimeroceras falcisulcatum* BECKER und *Acri. stella* n. sp., welche innerhalb einer Biozone episodisch in den Ablagerungsraum einwanderten. Die taxonomische Komplexität und Diversität in der Unterfamilie ist erheblich größer, als bisher angenommen. Gehäusemerkmale und geringe Variabilität stützen eine autökologische Interpretation der Paratornoceratinae als vollpelagische, aktive Schwimmer, die sich nach dem Aussterben oxyconer Tornoceratidae graduell aus suprabenthischen frühen Dimeroceratinae entwickeln konnten. Größenverteilungen zeigen, dass die Gehäuse anders als andere Ammonoideen zeitlebens wuchsen, ohne dass eine feststehende Maximalgröße erreicht wurde.

Abstract

Oxyconic members of the Dimeroceratidae (Goniatitida, Tornoceratina) are included in a new subfamily, the Paratornoceratinae n. subfam. The group occurred globally in almost all rich ammonoid faunas of the higher part of Upper Devonian II (UD II-F to II-I, Nehdenian). Two systematically excavated populations from Dar Kaoua in the central part of the Tafilalt (eastern Anti-Atlas, Morocco) are morphometrically analyzed as an example to clarify the significance of intraspecific variability, potential chronomorphoclines and of distribution patterns in a supposedly species-poor but variable oxyconic ammonoid group. Results showed that there are two clearly distinct species, *Acrimeroceras falcisulcatum* BECKER and *Acri. stella* n. sp. which immigrated the region episodically within one zone. Taxonomic complexity and diversity is much higher in the group than previously assumed. Shell features and restricted variability support an autecological interpretation as fully pelagic active swimmers which could evolve gradually from suprabenthic Dimeroceratinae after the extinction of oxyconic Tornoceratidae. Size distributions suggest that shell growth continued throughout life without reaching a final maximum diameter unlike in other ammonoids.

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Text-Fig. 1.

Known global distribution of Paratornoceratinae n. subfam. (black dots.).

S. AM. = South America; N. AM. = North America; N. EUR. = Northern Europe; S. EUR. = Southern Europe; KAZ. = Kazakhstan; KO. = Kolyma; eastern Siberia; TM. = Tarim Basin; TB. = Tibet; N. CH. = North China; J. = Japan; S. CH. = South China; B. = Burma; MA. = Malaysia; IC. = Indochina Block; NZ. = New Zealand; MAD. = Madagascar.

Migration of faunas occurred via the Prototethys and into the Uralian seaway.

1. Introduction

The taxonomy and phylogeny of ammonoids in general is affected by the often unsolved question of intraspecific variability and ecophenotypic differentiation of morphotypes versus genotypic change leading to associations and successions of closely related true species. A.S. DAGYS & W. WEITSCHAT (1993) have documented a large variability from compressed smooth oxycones to depressed, ribbed subcadicones in a population of the Triassic *Czekanowskites rieberi* DAGYS & WEITSCHAT which came from a single limestone concretion. Later (A. CHECA et al., 1996) it was shown that there is co-variation of specific characters but the feeling remained that similar patterns occur currently unrecognized in many other ammonoids. In the Devonian, populations from single beds have very rarely been studied morphometrically although results can affect taxonomy, stratigraphy, phylogeny, paleoecological interpretation and the question of phyletic gradualism versus migrational events. Specialists know that single assemblages may contain associated variable taxa as well as invariable forms, but documentation is poor.

In the early Famennian, there is a long known oxyconic member of the Dimeroceratidae which, under a range of generic names (*Aganides*, *Brancoceras*, *Dimeroceras*, *Paratornoceras*), was usually assigned to *Goniatites lentiformis* SANDBERGER (1857). Early workers such as R. WEDEKIND (1918, p. 150) emphasized its variability. Related forms have been described from various regions of the world such as the Rhenish Slate Mountains, Harz Mountains, Thuringia, Franconia, Saxony, Holy Cross Mountains, Montagne Noire, the Pyrenees, Cantabrian Mountains, northern and southern Morocco, Novaya Zemlya, eastern Urals, and NW Australia. Records are still lacking from Iran and North Chinese faunas (Text-Fig. 1).

In some regions, different species names were given. J. KULLMANN (1960: three subspecies) and M.S. PETERSEN (1975), however, assumed that all forms belong to just one species (*lentiforme*). J. KULLMANN (1960: *Dimeroceras lentiforme sobolevi* nom. nov.) even included the genus *Polonites* of B.I. BOGOSLOVSKIY (1957) which was based on *Dimeroceras lentiforme* SOBOLEV (1914) [non SANDBERGER!], and which was defined by a pointed and narrow rather than wide and rounded external (subumbilical) lateral lobe. In his review of German and North African paratornoceratids, R.T. BECKER (1993a) distinguished a new Moroccan genus, *Acrimeroceras*, with single v-shaped rather than tripartite dorsal lobe and kept a distinction between ribbed German *Paratornoceras acutum* (MÜNSTER) (including *lentiforme*) and Polish *Parat. polonicum* (GÜRICH). However, large variability and different morphotypes were again recognized in material from the Enkeberg type locality of *lentiforme*, especially with respect to whorl thickness, umbilication and ribbing. It was also emphasized that oxyconic Dimeroceratidae are not restricted to a single level but that they occur in at least four different zones (UD II-F to II-I) in the early Famennian (Upper *rhomboidea* to Upper *marginifera* conodont zones).

The paratornoceratids represent a goniatite group that can serve as an example to study the intraspecific variability in oxycones, to investigate the morphological distinction of widely separate populations and to search for chronomorphoclines in evolution. As an initial step, collecting of successive levels in the Tafilalt of southern Morocco provided two large populations that are suitable for morphometric analyses. Statistical results enable tax-

onomic conclusions which, however, require a brief review of some previously established taxa.

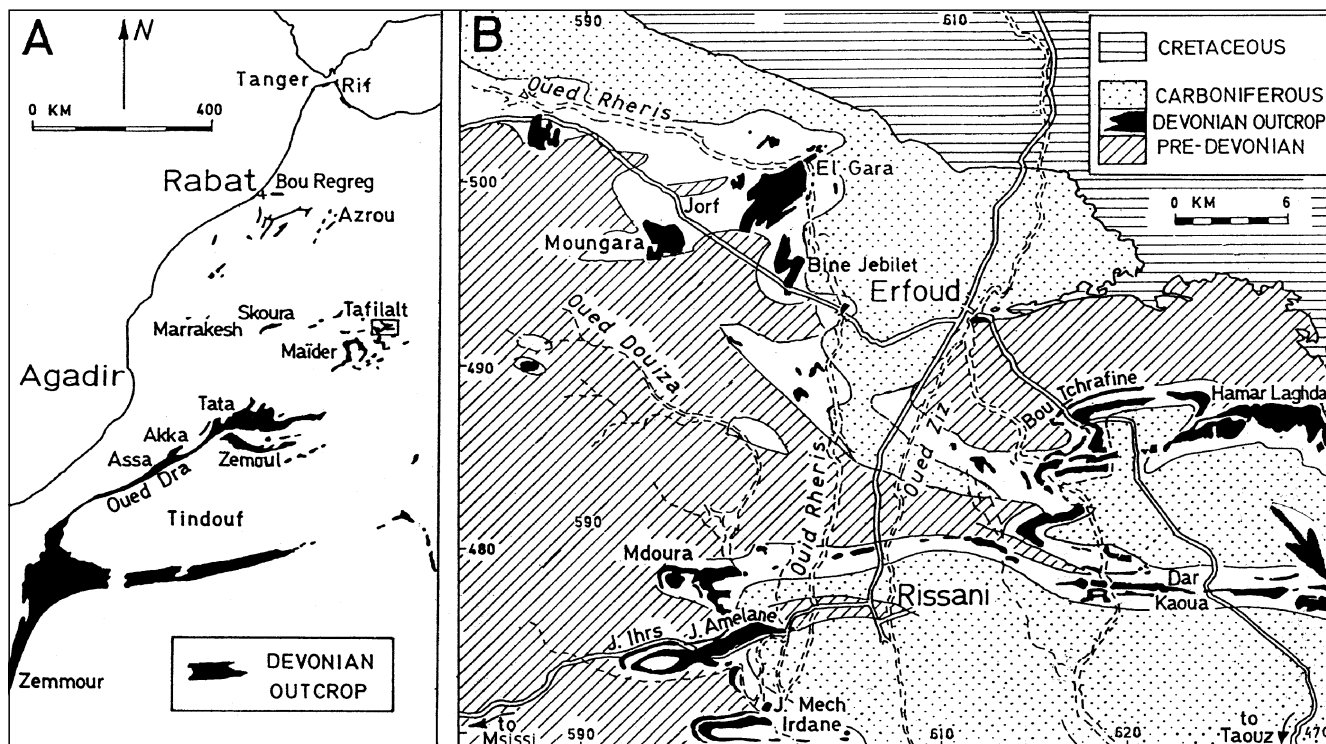
Abbreviations

E = ventral or external lobe; A = adventitious flank lobe; L_e = outer (subumbilical) lateral lobe; L_i = inner lateral lobe; I = dorsal or internal lobe; dm = diameter; ww = whorl widths; wh = whorl height; ah = apertural height; uw = umbilical widths. Upper Devonian ammonoid zone abbreviations follow R.T. BECKER (1993b).

2. Locality and Methods

The Anti-Atlas of southern Morocco is famous for its rich fossiliferous outcrops of Palaeozoic strata. Systematically excavated populations came from Dar Kaoua, 18.5 km SE of Erfoud (Text-Fig. 2), in the central Tafilalt. In palaeogeographic terms, the section lies at the transition from strongly condensed cephalopod limestones of the Tafilalt Platform to more argillaceous facies of the Tafilalt Basin. The section was investigated in detail by R.T. BECKER (1993a, see for further literature) who illustrated a latest Frasnian (*Crickites holzapfeli* Zone, UD I-L) to late lower Famennian (*Maeneceras "biferum"* Zone, UD II-G) succession dipping with 26–29° to the south. Younger strata are poorly exposed in the plain to the south. Oxyconic dimeroceratids were originally found in Beds F, H, J and K (Text-Fig. 3), but there were only single specimens each from Beds F and K and subsequent excavations could not repeat these findings. Field work, therefore, concentrated on the massive Bed H and on the platy Bed J which both consist of yellow-brown to reddish fine micrite with mass occurrence of well-preserved pelagic fauna, such as goniatites, orthocones, rhynchonellids, pelecypods and ostracods. Updated faunal lists for restudied beds are given in Text-Fig. 3. The diversity of ammonoid species, despite their abundance, is low. The slightly nodular Bed F differs from Beds H and J in the general scarcity of goniatites and by a peculiar enrichment of pelecypods in its lower part suggesting deposition during a shallowing phase. In lenticular enrichments, some goniatites (*Cheiloceras*, *Armatites*) occur together with abundant trilobite remains (*Trimeroccephalus*, *Calybole*). *Calybole* (s.str., excluding *Skemmatocare* and *Prodiacoryphe*) is recorded here for the first time from North Africa.

Bed H yielded 113, Bed J 164 oxyconic goniatites. All measurements (in mm) were obtained with a digital slide rule; taken parameters are explained in Text-Fig. 10. Prior to the comparison of both data sets, the accuracy of measurement was studied according to ISO (International Organization for Standardization) 5725, accuracy (trueness and precision) of measurement methods and results, part 1–6. This was accomplished by measuring one specimen from Beds H (No. 79) and two specimens from Bed J (No. 50 and 21) independently ten times by two persons (VE and JB). Mean values (\bar{x}_m), the standard deviation of results obtained under repeatability conditions (s_r) or under reproducibility conditions (S_R), the repeatability (r) and the reproducibility (R) with a statistical significance of 95 %, were calculated (Tab. 1). The repeatabilities (r) were in the range of 0.2 to 1.2, the reproducibilities (R) in the range of 0.4 to 1.6. Precise measurements of the apertural height of small specimens turned out to be most difficult. The variance of measurements is not homogenous and mean values show significant differences. Hence, the investigation of changes of apertural height during ontogeny is better accomplished using median cross-sections.



Text-Fig. 2. Geographical and geological position of the sampled section at Dar Kaoua in the eastern Anti-Atlas (R.T. BECKER & M.R. HOUSE, 1994: Fig. 1, slightly altered).

A: Position of the Tafilalt in NW Africa; B: position of the measured section (arrow) at the E-W-running Dar Kaoua ridge.

Specimen No. 50 (Bed J)

	dm	wh	ww	ah
n	10	10	10	10
\bar{x}_m (mm)	7,82	4,45	5,78	1,62
s_r	0,171	0,427	0,06	0,097
s_R	0,211	0,577	0,063	0,420
r	0,478	1,197	0,167	0,272
R	0,589	1,615	0,177	1,177

Specimen No. 21 (Bed J)

	dm	wh	ww	ah
n	10	10	10	10
\bar{x}_m (mm)	29,6	18,05	12,82	8,87
s_r	0,132	0,314	0,342	0,265
s_R	0,128	0,316	0,485	0,292
r	0,369	0,880	0,956	0,742
R	0,359	0,886	1,358	0,818

Specimen No. 79 (Bed H)

	dm	wh	ww	ah
n	10	10	10	10
\bar{x}_m (mm)	42,03	25,60	10,52	14,71
s_r	0,340	0,258	0,146	0,222
s_R	0,332	0,364	0,141	0,258
r	0,951	0,722	0,409	0,622
R	0,982	1,018	0,396	0,722

3. Morphometric Analyses of Dar Kaoua Paratornoceratinae

3.1. Size Distribution

The two populations give insights into aspects of ammonoid growth and size in a very fine-grained depositional environment where current sorting and transport of dead shells has been minimal. Size distributions are plotted as histograms in Text-Fig. 4. The assemblage from Bed H shows a mean size of 37 mm dm, whereas the population from Bed J consists on average of smaller specimens (mean at 22 mm dm). Supported by analyses of other shell parameters (see below), there is no evidence of dimorphism. The frequency curves of both populations are roughly symmetrical in the middle part and give a Gaussian distribution. Since there is no indication of synchronous mass mortality, the presence of size classes reflecting different annual generations was not expected. The rarity of small specimens indicates low mortality of juveniles, at least of those who were not eliminated from the fossil record by complete predation. The size distribution curves become highly asymmetric towards larger diameter, based on a minority of large to single extremely large specimens ("megaconchs") which reach a size

Table 1. Accuracy of shell parameter measurements following ISO 5725 in three paratornoceratines from Beds H and J, based on repeated ($n =$ ten times) independent trials of two persons (VE and JB).

\bar{x}_m = mean value; s_r = standard deviation under repeatability conditions; s_R = standard deviation under reproducibility conditions; r = repeatability; R = reproducibility.

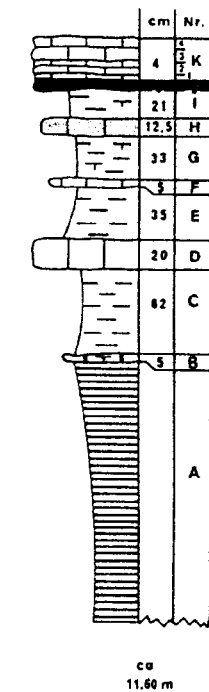
Text-Fig. 3.

Sedimentary and faunal succession in the early Famennian at Dar Kaoua, based on R.T. BECKER (1993a) and on new collections. Records of *Calybole* (s.str.) are new for North Africa.

nearly seven times as much as the mean value but which show otherwise no morphological modifications. This strongly suggests in both populations, but unlike in *Nautilus* (P.D. WARD, 1987) or in many other ammonoids (H. BUCHER et al., 1996), including Carboniferous goniatites (W. MANGER et al., 1999b), that growth continued unconstrained throughout life without reaching a fixed maximum size, for example controlled by reproduction cycles. Obviously only few specimens managed to reach very old age.

In paraturnoceratines there is no clearly defined adult stage with morphological specialisation that would require a "count-down" of growths (A. SEILACHER & P.Y. GUNJI, 1993) or a prescribed final morphogenetic programme, controlled by hormone release and gonad growth. The smooth Gaussian distribution pattern contradicts an interpretation that only few pathological individuals with delayed or inhibited sexual maturation kept growing, as was postulated for some Carboniferous goniatites (W.L. MANGER et al., 1999a). There is also no obvious systematic reduction of septal spacing in large specimens which would suggest a general reduction of growth speed at maturity. Larger specimens neither show obvious wider septal spacing which would point to a possible, ecologically controlled, large variability in growth speed. This, anyway, would be difficult to explain in a single population living under the same environmental conditions. The latter aspect also speaks against externally triggered large differences in time of maturation (K. MANGOLD, 1987) which may occur in populations of one taxon living in widely different facies. For example, pyritic black shale faunas tend to be smaller sized than con-

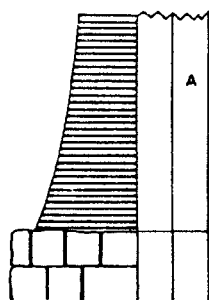
DAR KAOUA



Acrimeroceras falcisulcatum
Armatites planidorsatus
Cheiloceras (Raymondiceras) lagowiense
Maeneceras subvaricatum nuntio
Buchiola sp.
Perrarisinurostrum sp.
 ostracods, crinoids

Acrimeroceras stella n.sp.
Maeneceras subvaricatum subvaricatum
Armatites planidorsatus
Falcitornoceras aff. *bilobatum*
"Terebratula" rotundata
 rhynchonellids, ostracods, crinoids

[*Acrimeroceras stella* n.sp.]
Cheiloceras sp.
Armatites planidorsatus
Calybole cf. *denckmanni*
Trimeroccephalus lelievrei
 ostracods, crinoids, rhynchonellids
 various pelecypods

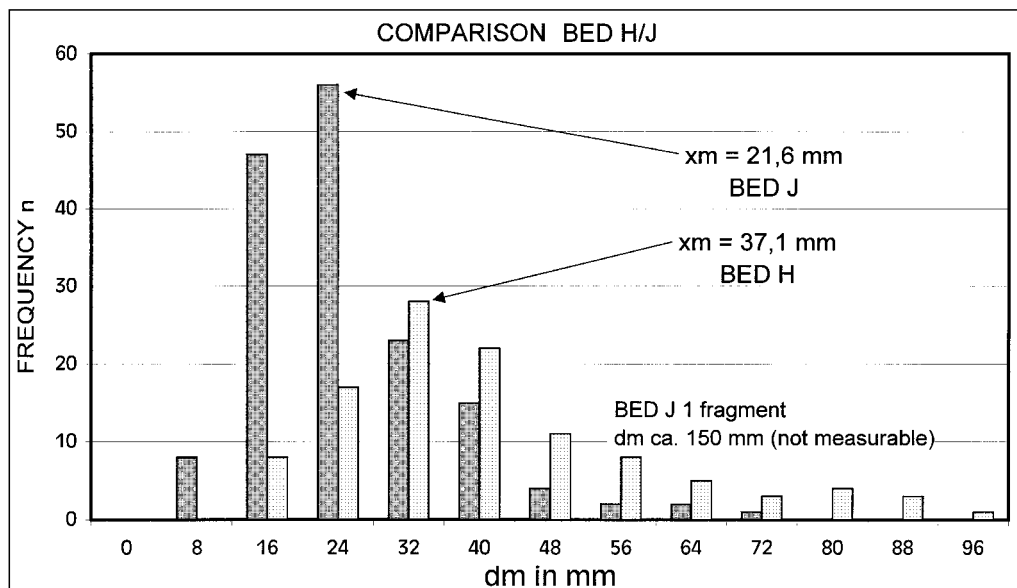


Gephuroceratiden indet.

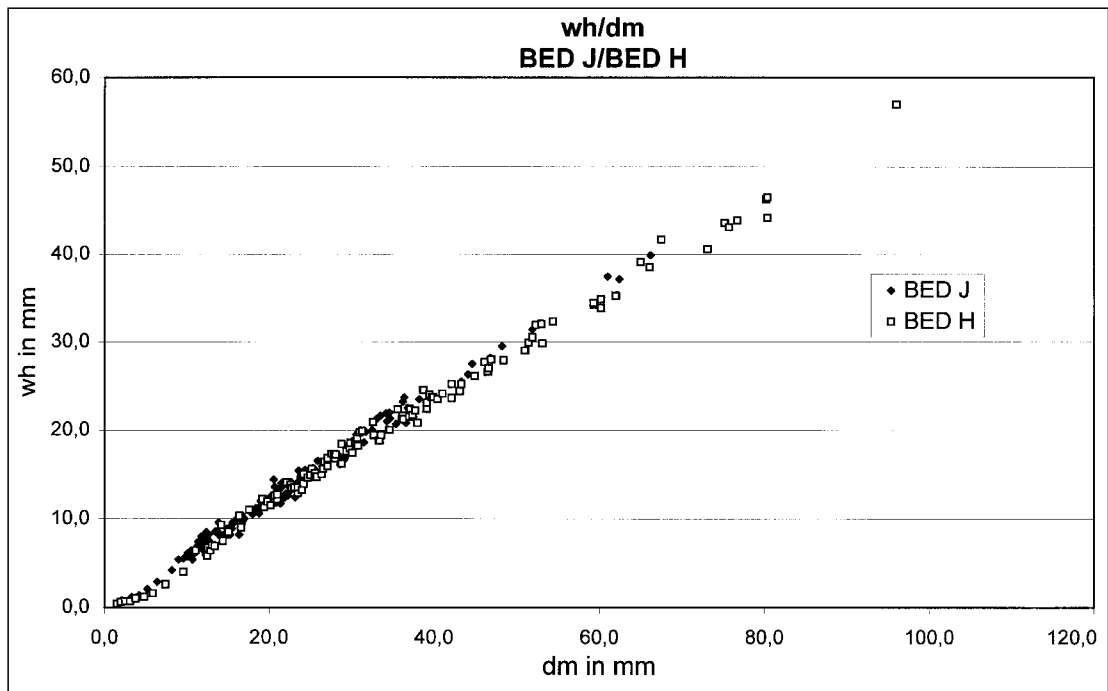
FAMENNIAN
 FRASNIAN

Text-Fig. 4.

Size histogram of the two populations from Beds H and J, showing the larger average size (x_m) in Bed H and the indeterminate growths of a minority of non-dimorph "megaconchs" (up to ca. 150 mm Ø).



Text-Fig. 5.
Statistical analyses of
the wh/dm ratio in
Bed H and J popula-
tions.

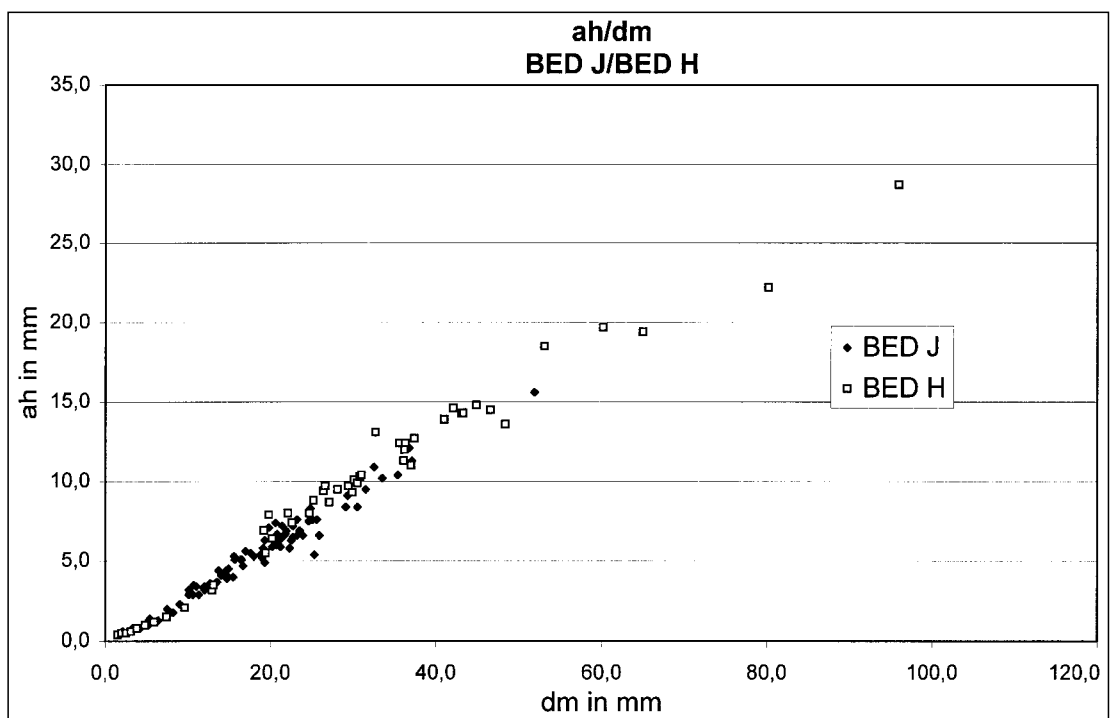


specific assemblages of well oxygenated limestone facies. Shell preservation covering sutures, unfortunately, has not yet allowed a statistical analyses of septal formation. Factors limiting gradually life span and growths could have been diseases, gerontic deteriorations and available food resources; large individuals with their fast (exponentially) increasing body mass would have had significantly higher metabolic rates.

3.2. Shell Parameters

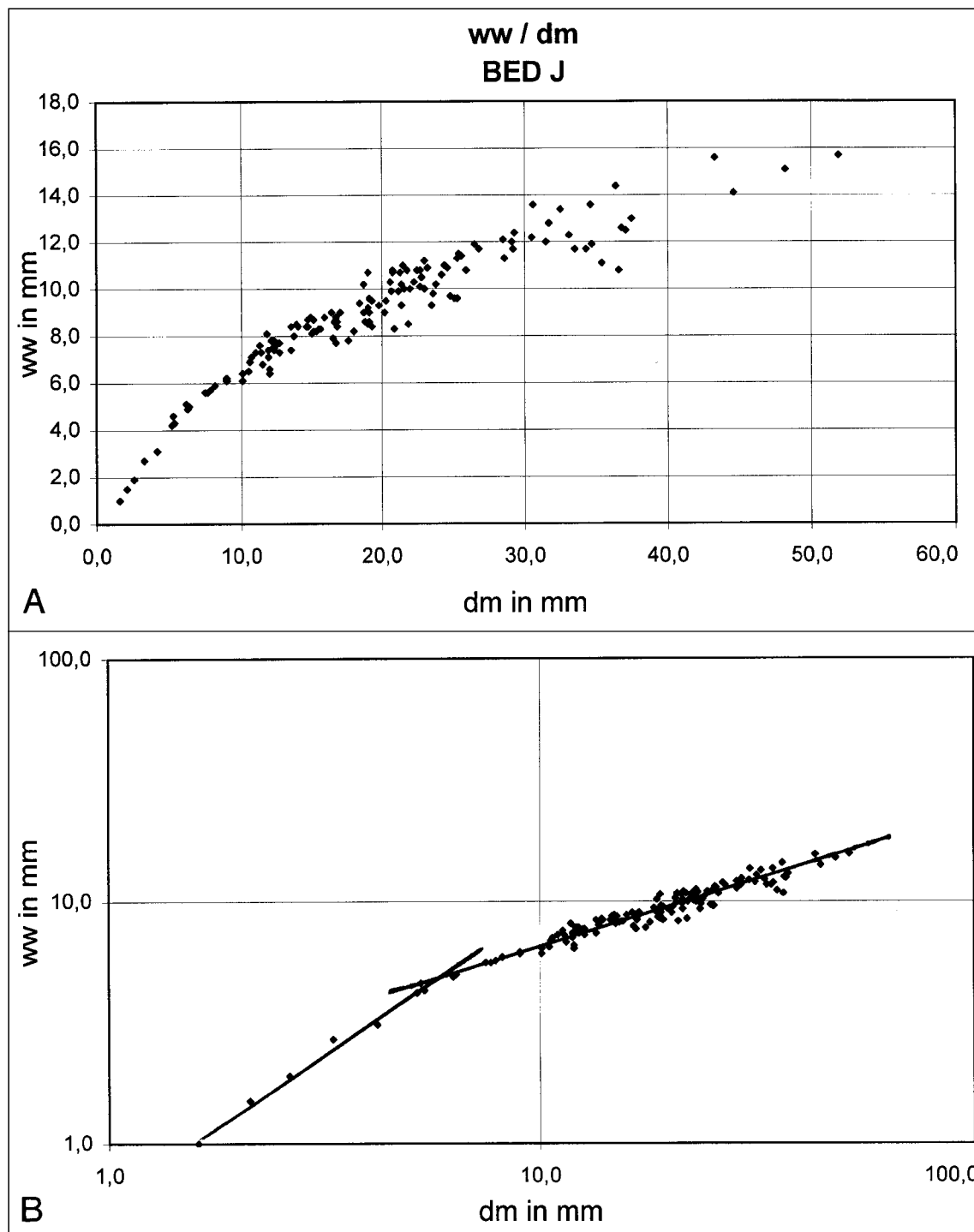
Text-Figs. 5–6 show statistical analyses of the relative whorl height and apertural height (wh/dm and ah/dm) throughout ontogeny. In involute shells, both parameters are indicators of whorl expansion rates which is shown to be approximately identical and constant in both popula-

tions. The extremely large individuals are no exception which gives evidence that they belong to the same taxa and that large size is not reached by faster growth of the whorl spiral. There is a significant ontogenetic change in the first whorls up to ca. 10 mm dm with a sudden increase in both measured ratios based on the closure of the juvenile open umbilicus and based on the change from evolute depressed early whorls to involute, compressed sub-mature stages. Due to the lack of small specimens, this diphasic growth or change of allometric constants (see R. KANT & J. KULLMANN, 1988) is best visible in comparison of cross-sections (Text-Fig. 10) or of small individuals (Text-Fig. 12). In the population from Bed J, the umbilicus closes earlier leading to an earlier onset of higher wh/dm ratios (Text-Fig. 5). The juvenile change to higher apertures (ah/dm) is more similar in the two faunas (Text-Fig. 6).



Text-Fig. 6.
Statistical analyses of
the ah/dm ratio in Bed
H and J populations.

Text-Fig. 7.
Statistical analyses of the ww/dm ratio in the Bed H population (*Acri. stella* n. sp.) using linear (A) and double logarithmic (B) plots.

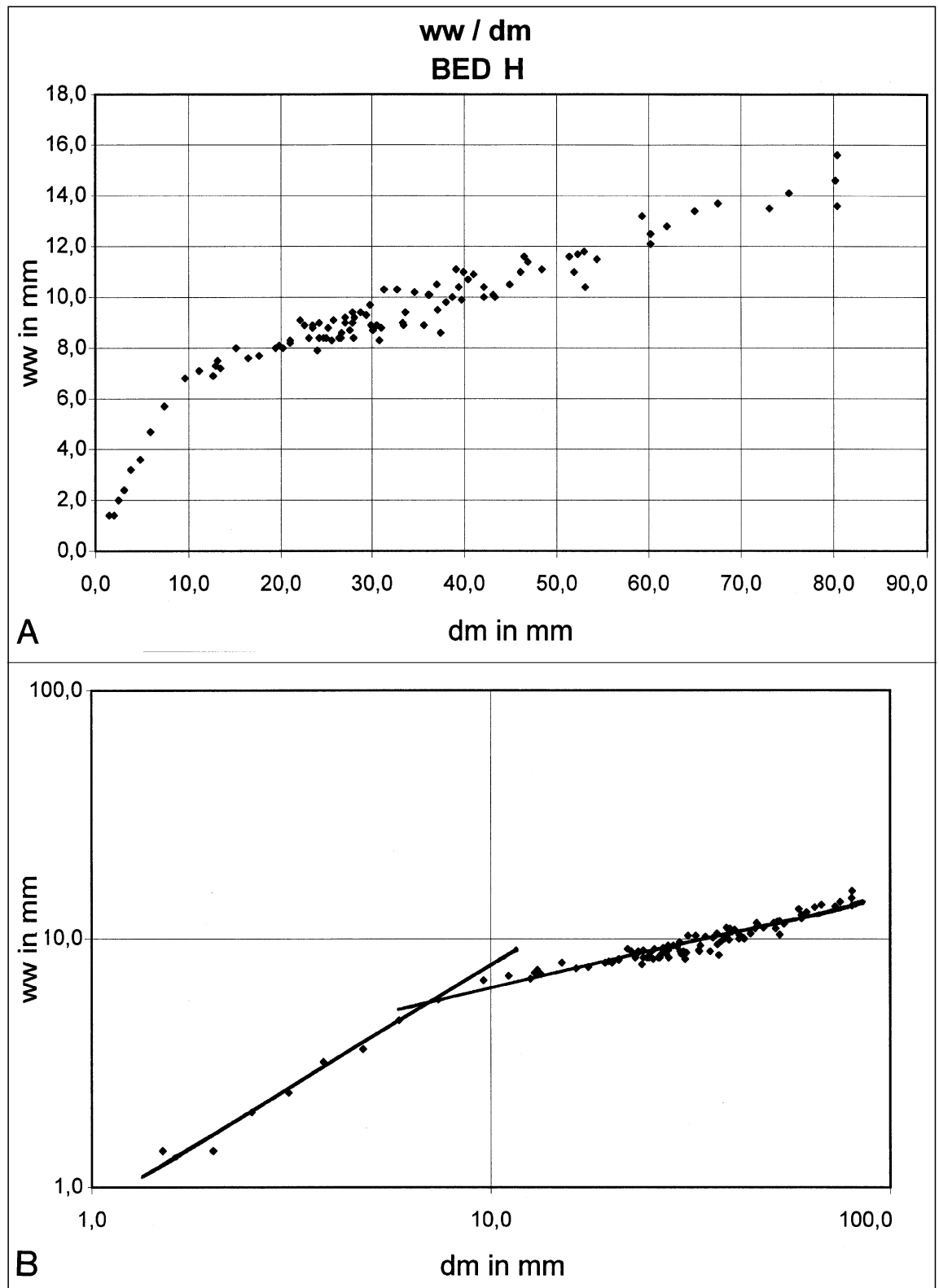


A much clearer distinction between both assemblages, even excluding the confusion of loose material from the two units, is based on the comparison of ontogenetic changes in relative whorl widths. Text-Figs. 7 and 8 illustrate the two populations both in linear and logarithmic plots. The latter clearly show only slight deviations of individual plots from regression linears, with sudden changes in the allometric constants of the conch between eight and nine mm dm. Such diphasic growth (with "accentuation of Rd [= dm] in the second phase") has been illustrated for a "*Dimeroceras*" by R. KANT & J. KULLMANN (1988) who, however, showed an ontogenetically much younger break. This may reflect that a different paratornoceratid population and species has been used; allometric constants and their angles in logarithmic plots can be used for taxonomic definitions, but identical scales must be used. In logarithmic

plots, the majority of median-sized to large specimens falls in a rather small field and the significant difference in ontogenetic whorl widths development, without overlap of both populations from ca. 15–20 mm dm on, is much better visible in a plot of absolute measurements (Text-Fig. 9).

The statistical analyses of shell parameters indicates that the two oxyconic faunas belong to two different but related morphospecies of *Acrimeroceras*, one of which is new (Bed H: *Acri. stella* n. sp.), and one of which (Bed J) is conspecific with the holotype of *Acri. falcisulcatum* from Bine Jebilet of the northern Tafilalet (R.T. BECKER, 1993a). As outlined in the following chapter, additional shell features such as ornament and varices confirm this interpretation. Apart from the differences between populations, the variability of shell parameters is rather restricted in these

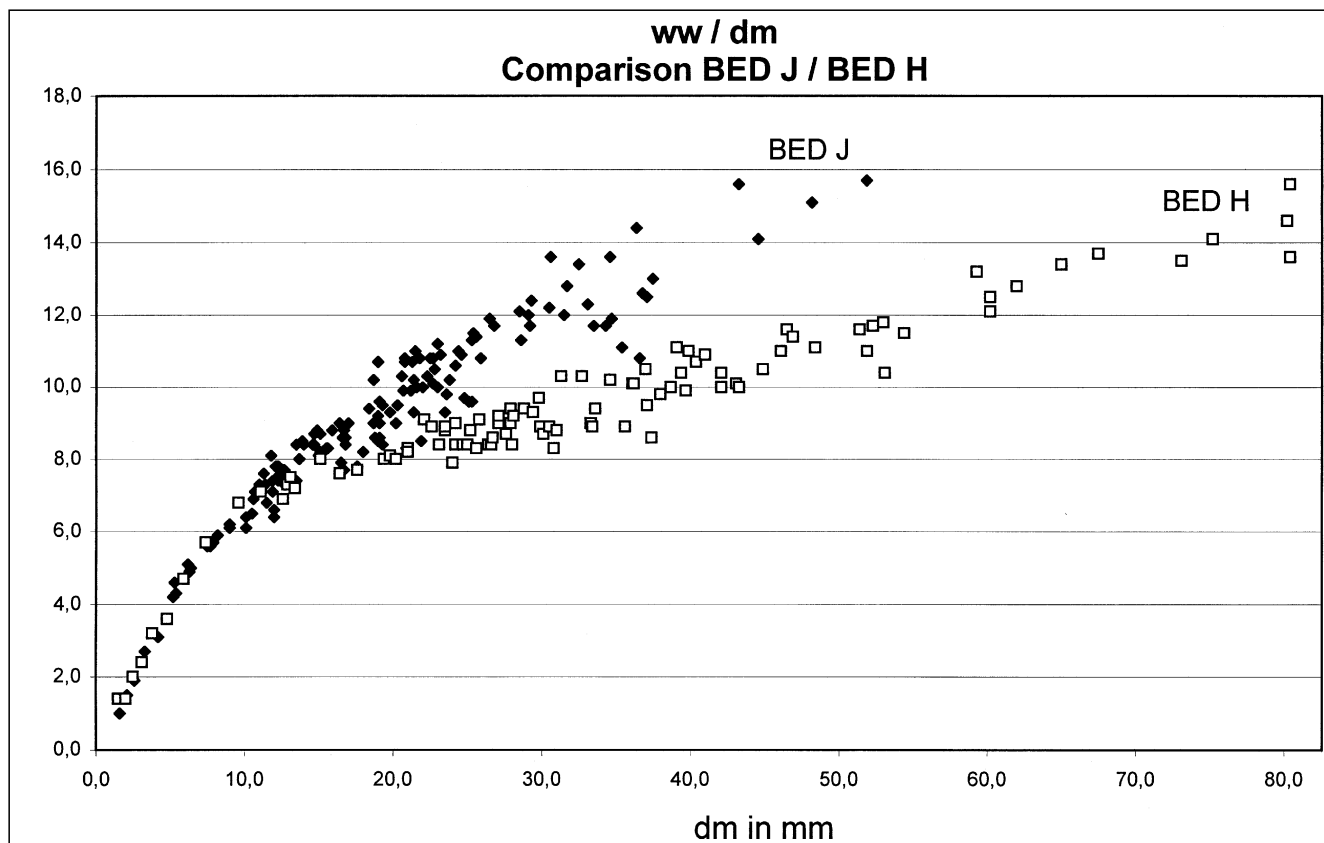
Text-Fig. 8.
Statistical analyses of the ww/dm ratio in the Bed J population (*Acrit. falsiculatum*) using linear (A) and double logarithmic (B) plots.



oxyconic forms, unlike as in the Triassic *Czekanowskites* of A.S. DAGYS & W. WEITSCHAT (1993). The lack of intermediate specimens and the identical litho- and biofacies of both limestones that yielded the population speak against an interpretation as two environmentally controlled morphotypes of a single species. There was no chronomorphocline in Moroccan paratornoceratines and the taxonomic diversity in the oxyconic group was obviously much larger than previously known. This requires a restudy of related forms from other regions of the world.

4. Systematics

Order:	Goniatitida HYATT
Suborder:	Tornoceratina WEDEKIND
Superfamily:	Dimerocerataceae HYATT
Family:	Dimeroceratidae HYATT
Subfamily:	Paratornoceratinae BECKER n. subfam.



Text-Fig. 9.

Comparison of the ww/dm ratios in Bed H and J populations showing the clear distinction of two taxa from median stages (ca. 15 mm dm) on.

Diagnosis: Shell with open umbilicate depressed early and compressed, fast expanding, involute oxyconic to lanceolate median and adult stages; body chamber length ca. one whorl (slightly mesodomic), growth lines convex to weakly biconvex. Sutures with divided lateral lobe, deep and pointed A_1 -lobe and sometimes with incipient A_2 -lobe; dorsal lobe tripartite or (secondarily) deep, narrow and v-shaped; sutural formula: $E(A_2)A_1L_e : L_1(l_2)l_1$.

Remarks: The stratigraphical and morphological sequence from rather thick *Paratornoceras* with tripartite dorsal lobe of the *Parat. lentiforme* Zone (lower UD II-F) to thinly oxyconic *Acrimeroceras* with unified dorsal lobes of the *Maeneceras* Zone (upper UD II-F and II-G), and eventually to very compressed *Polonites* with narrow L_e -lobe from the *Dimeroceras* Zone (UD II-I, R.T. BECKER, 1993a) gives empirical evidence for an oxyconic phylogenetic lineage within the Dimeroceratidae. The main stock of dimeroceratid evolution led from *Praemeroceras* via *Dimeroceras* to adult open umbilicate *Paradimeroceras* (R.T. BAECKER, 1993a) with still depressed and slowly evolving whorls and pointed L_e -lobe. This diverging phylogeny should be expressed taxonomically by the recognition of two separate subfamilies.

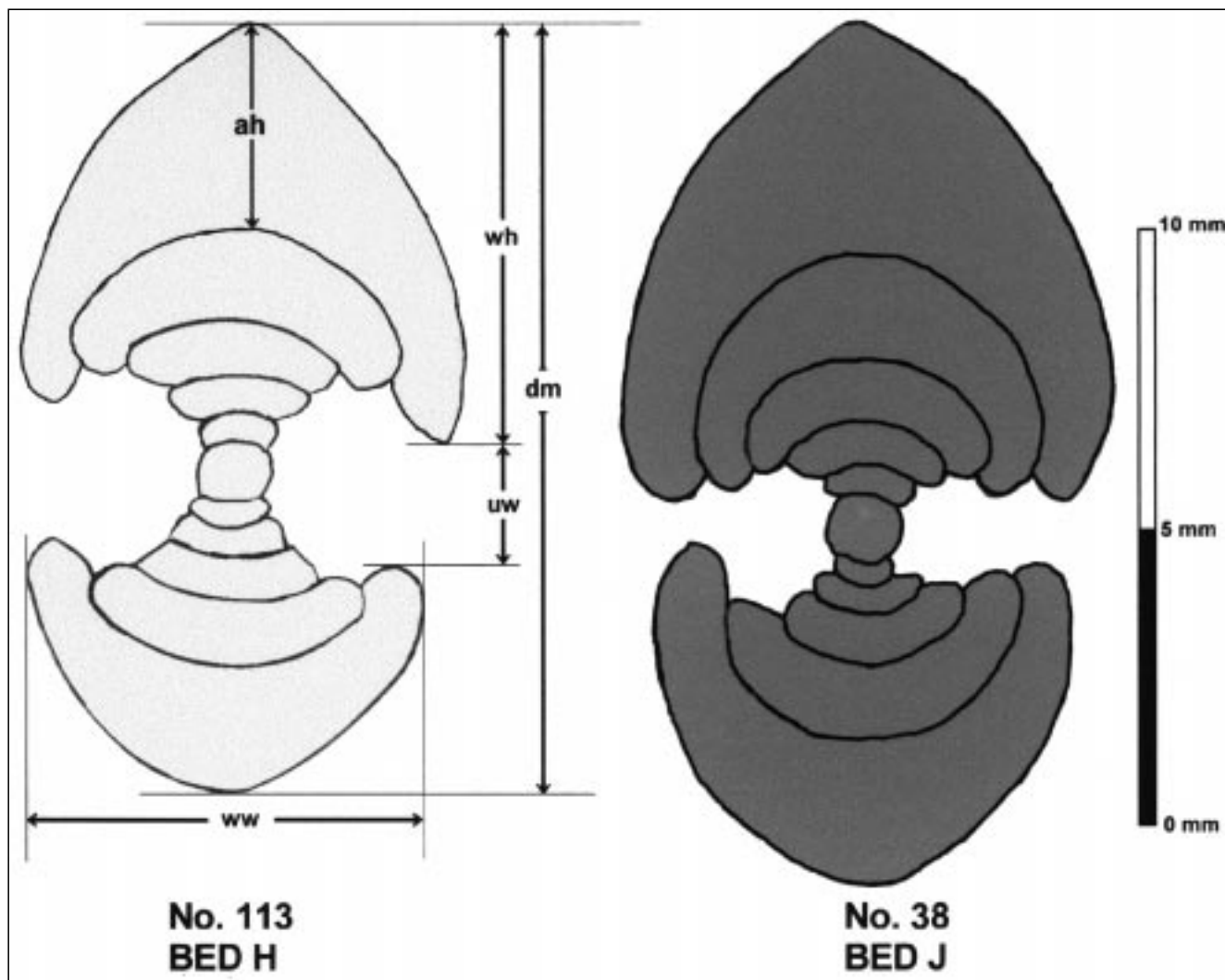
Acrimeroceras BECKER, 1993

Type-species: *Acri. falcisulcatum* BECKER, 1993.

Diagnosis: Early stages depressed, subglobular, smooth or ribbed, with open umbilicus and with rounded to suboxyconic venter; the venter sharpens relatively early in ontogeny; adult stages extremely compressed, smooth, oxyconic to lanceolate. Sutures with widely rounded L_e -lobe, pointed wide and asymmetric A -lobe,

and with incipient second A -lobe formed by a step in the ventral branch of A_1 , dorsal lobe secondarily simple, narrow and v-shaped; sutural formula: $E(A_2)A_1L_e : L_1l_1$.

Remarks: Paratornoceratines from the Holy Cross Mountains (G. GÜRICH, 1900: Pl. XIV, Fig. 3a–b), the Urals (B.I. BOGOSLOVSKIY, 1971: Text-Fig. 58) and from the Canning Basin (M.S. PETERSEN, 1975: Pl. 3, Fig. 5) were shown to possess a trifid dorsal suture. The simple and narrow dorsal lobe found in Moroccan oxyconic dimeroceratids was, therefore, used as a criterion for generic separation. The new knowledge of taxonomic complexity in the subfamily requires a restricted use of species names and clear definitions. Unfortunately, the dorsal suture of *Gonialites lentiformis* from Enkeberg, the type-species of *Paratornoceras*, has never been illustrated although R. WEDEKIND (1908) referred to G. GÜRICH's (1900) illustration. The original description of *Gon. lentiformis* does not give many details of shell form and ornamentation and only mentions the presence of mould constrictions. Collections at the Museum für Naturkunde and previous descriptions show that a wide range of paratornoceratines are present at the type-section which could belong to up to four different species of *Paratornoceras*, *Acrimeroceras* and *Polonites*. Since SANDBERGER's types could not be traced, and in order to stabilize generic nomenclature in the subfamily, topotypic MB.C.2859, a median-sized specimen with sharp venter and open umbilicus, without any trace of ribbing, but showing clearly a trifid dorsal suture is here selected as neotype. Its measurements are as follows: dm 22 mm (thus in the scale of SANDBERGER's types), wh 11.3 mm, uw 3.3 mm, ww 10.2 mm, ah 6.6 mm. The suture is illustrated in Text-Fig. 13. A further revision of *Paratornoceras* including rich new Canning Basin material will be published elsewhere.



Text-Fig. 10.

Comparison of cross-sections of *Acrir. stella* n. sp. (Bed H: MB.C.2872) and of *Acrir. falcisulcatum* (Bed J: MB.C.2873) showing the faster closure of the umbilicus in the latter species.

Included species: *Acrir. falcisulcatum* BECKER, *Acrir. stella* n. sp., *Acrir. n. sp. 1* from the Canning Basin, *Acrir. n. sp. 2* from Germany, *?Goniatites acutus* (MÜNSTER), a nomen dubium.

Stratigraphical Range: Upper part of UD II-F to II-H.

Distribution: Rhenish Slate Mountains (Enkeberg), ?Harz Mountains, ?Thuringia, ?Franconia, ?Saxony, Tafilalt, ?Montagne Noire, ?Pyrenees, ?Cantabrian Mountains, Canning Basin (R.T. BECKER & M.R. HOUSE, 1997). The taxonomic position of compressed Paratornoceratinae from the upper part of II-F and II-G (*marginifera* Zone) from most German, French and Spanish localities needs revision but, based on collections of W. PAECKEL-MANN (1936: Bed 18), *Acrimeroceras* is clearly present in UD II-G of the famous Enkeberg section.

***Acrimeroceras falcisulcatum*
BECKER, 1993a (emend.)**

Type: Holotype Be 615 (now deposited at Senckenberg Museum, Frankfurt a.M., SMF 60.151) from Bine Jebilet, northern Tafilalt.

Diagnosis: Early stages subglobular, with rounded venter (up to ca. 10 mm dm), with rather narrow umbilicus,

and with convex growth lines; median (from ca. 10 mm dm on) to adult stages oxyconic, with closed umbilicus and with biconvex growth lines with very shallow flank sinus. A keel is formed in latest stages. Deep, mostly falcate mould constrictions are present throughout ontogeny and terminate at the ventral keel. Ribbing is always absent. Sutures with sharp, wide and asymmetric A-lobe that has a slight concavity (incipient A₂) in its ventral branch.

Stratigraphical Range: Lower part (Upper *Acrimeroceras* Beds = Beds DK/J-?K) of II-G.

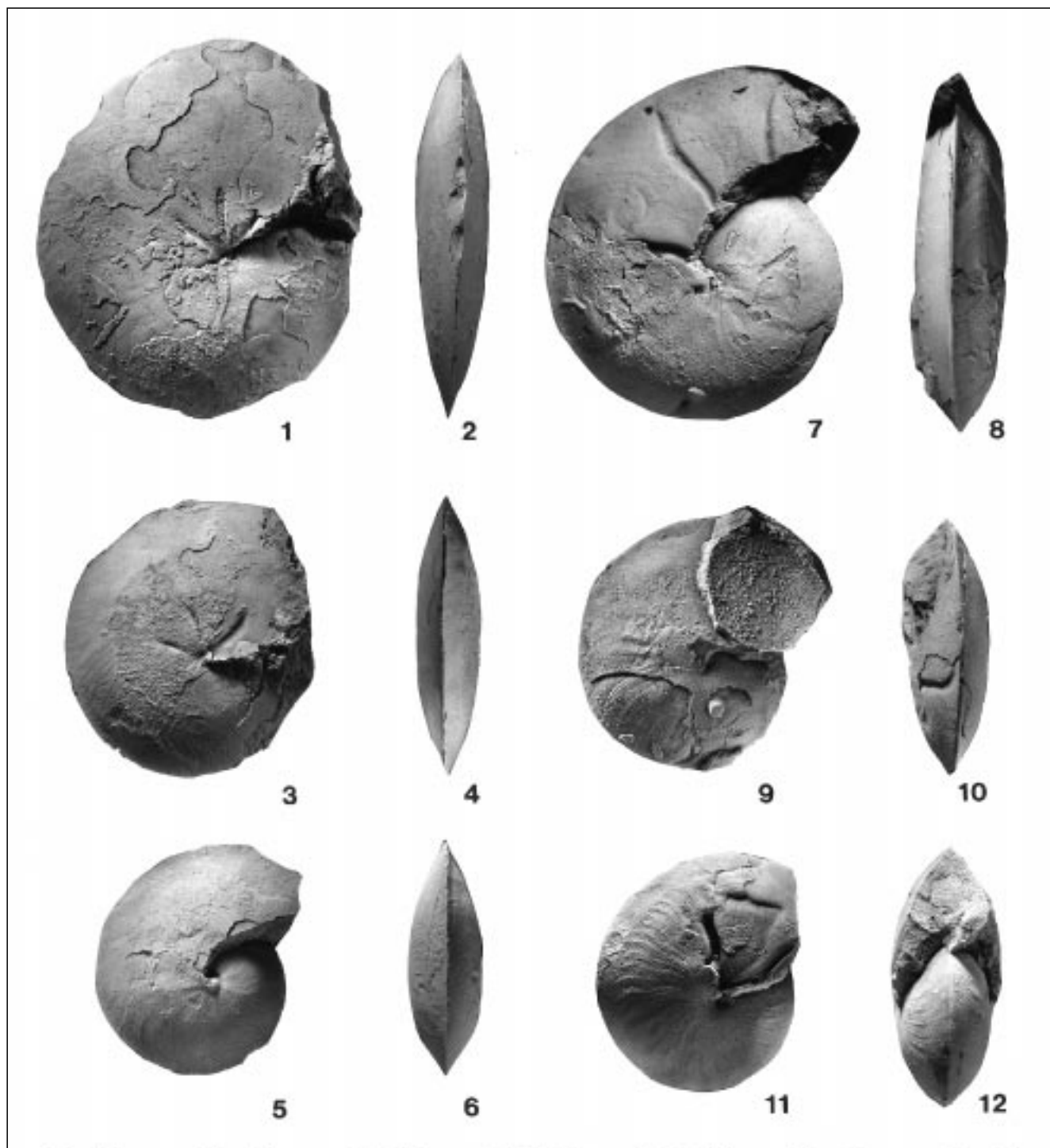
Distribution: Restricted to the Tafilalt.

***Acrimeroceras stella*
BECKER, BOCKWINKEL & EBBIGHAUSEN n. sp.**

Type: MB.C.2860, an adult specimen showing the typical constrictions (Text-Fig. 12.1-2) and extremely compressed, lanceolate shell form.

Derivation of name: According to the mould constrictions forming star-like impressions around the umbilicus.

Diagnosis: Early stages (up to 10 mm dm) subdiscoïdal, with rounded dorsolateral ribs (ca. 12 ribs on half a volution), wide umbilicus, sinuose mould constrictions



Text-Fig. 11.

Comparison of median and adult stages of *Acri. stella* n. sp. (1–6) and of *Acri. falcisulcatum* (7–12) showing the distinctive lanceolate venter and the star-like dorsolateral mould constrictions in the first species.

1–2: Holotype, venter with broken delicate ventral keel.

MB.C. 2860, $\times 1$.

3–4: Paratype, with typical constrictions.

MB.C.2861, $\times 1$.

5–6: Paratype, median stage with subconvex growth lines.

MB.C.2862, $\times 1.5$.

7–8: With typical extended constrictions and distinctive mature keel.

MB.C.2863, $\times 1$.

9–10: Showing the shallow flank sinus of growth lines, venter simply oxyconic.

MB.C.2864, $\times 1$.

11–12: Relative thick median stage with biconvex growth lines, deep mould constrictions and repaired gird-like shell fracture (forma substructa) near the aperture.

MB.C.2865, $\times 1.5$.

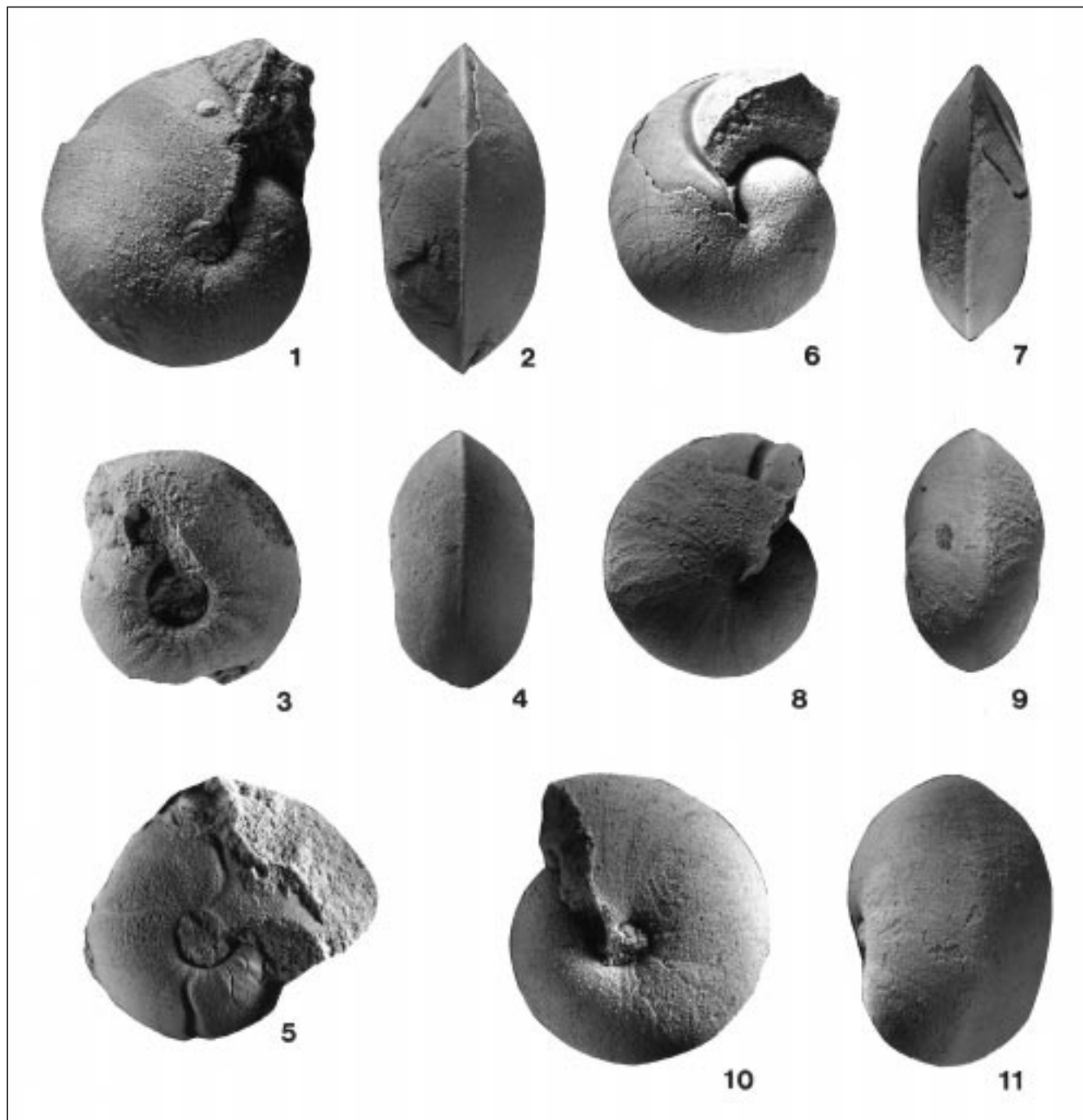
and with narrowly rounded to oxyconic (from ca. 7 mm dm on) venter; median to adult stages strongly compressed and lanceolate, constrictions are restricted to the inner flanks; the umbilicus closes at ca. 16 mm dm.

Description: The dimensions of the holotype are as follows: dm 62 mm, wh 35.2 mm, ww 12.8 mm. Further measurements can be taken from the plots in Text-Figs. 5–9. Many paratypes show Ritzstreifung on the mould which is strongest developed on the inner flanks.

The wrinkle layer on the outer shell of preceeding whorls is similar in both studied *Acrimeroceras* species; wrinkles project slightly from the closed umbilicus and follow a convex arch over the mid-flank, to pass then rather straight over the venter. Growth lines form inconspicuous bundles of ca. 1 mm widths. Only best preserved specimens (MB.C.2862) show a very fine crenulation of the delicate keel with ca. five crenulae/mm. Sutures are

illustrated in Text-Fig. 13.2–3. The body chamber angle seems to lie at ca. 350 to 360° giving a slightly meso-domic conch.

Comparison: The new species can easily be distinguished from the type-species of the genus by its more evolute and ribbed early stages, by the stronger shell compression, by the adult restriction of mould constrictions to the inner flanks, and by the stronger developed,



Text-Fig. 12.

Comparison of juvenile stages of *Acri. stella* n. sp. (1–5) and of *Acri. falciculatum* (6–11) showing the wider umbilicus and earlier ventral sharpening in juveniles of the first species.

1–2: Paratype, thick but oxyconic late juvenile stage with still open umbilicus.

MB.C.2866, $\times 3$.

3–4: Paratype, ribbed and widely umbilicate juvenile with keeled venter.

MB.C.2867, $\times 3$.

5: Paratype, juvenile mould with deep, biconvex constrictions and wide umbilicus.

MB.C.2868, $\times 3$.

6–7: Late juvenile involute stage with typical falcate constriction and biconvex growth lines.

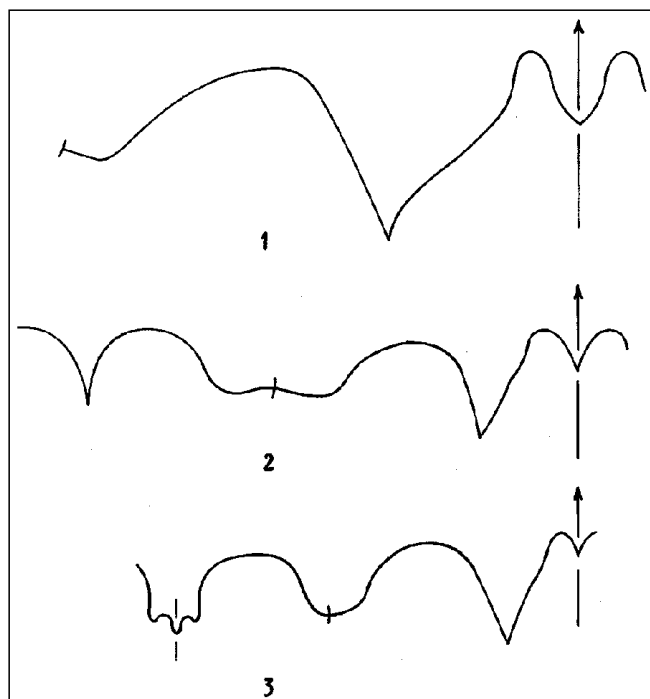
MB.C.2869, $\times 2$.

8–9: Juvenile with deep constriction, convex growth lines and slightly suboxyconic venter whilst the umbilicus is already closed.

MB.C.2870, $\times 3$.

10–11: Early juvenile with slightly open umbilicus, convex growth lines and well-rounded broad venter.

MB.C.2871, $\times 5$.



Text-Fig. 13.
Sutures of Paratornoceratinae.

- 1) *Acri. falciculatum*.
MB.C.2874, loose specimen, external suture at ca. 30 mm wh.
- 2) *Acri. stella* n. sp.
MB.C.2872, paratype, complete suture at ca. 24 mm dm.
- 3) *Parat. lentiforme*.
MB.C.2859, neotype, complete suture at ca. 22 mm dm.

razorsharp keel which leads often to characteristic peripheral breakage of shell parts during extraction from the bed.

Stratigraphical Range: ?Upper part of UD II-F to lower part of II-G (Lower *Acrimeroceras* Beds = Beds DK/?F,H).

Distribution: Restricted to the Tafilalt.

***Goniatites acutus* MÜNSTER, 1840**

Type: Holotype BSPHG VII 610, refigured by R.T. BECKER (1993a), Pl. 16, Figs. 11a–b.

Remarks: The holotype is extremely compressed and oxyconic as other *acrimero*ceratids but since sutures are not preserved, and in the light of the desired restricted use of names, recognition of the species seems impossible. The lack of constrictions and ribs give similarities with new Australian material but relationships with similarly thin German *Polonites* cannot be ruled out. At least at present, G. MÜNSTER's species is regarded as nomen dubium. Recent (summer 1999) examination of the Geyser type locality additionally showed that there is little hope of collecting better preserved topotypes in the future. Only light grey UD III micrites still yield *goniatites* in the area of the Zeyergrund.

Stratigraphical Range: Probably UD II-G.

5. Palaeoecological and Phylogenetic Aspects

The restricted variability of shell parameters proves that there was strong selective pressure on conch shape and cross-section, most likely in order to reduce drag during swimming. The slightly mesodomic body chamber, the

evolutionary trend towards increasing sutural complication, thin shell walls, and the involute and streamlined, razorsharp oxyconic shape of the conches are important features that suggest a strictly pelagic, free-swimming, vertically migrant lifestyle of paratornoceratines (compare with the interpretation of oxycones in G.E.G. WESTERMANN, 1996). This is in accord with a rather broad environmental range of members of the subfamily, from laminated and hypoxic black shale basins (southern Morocco), deep-water clastic turbidite regions (northern Rhenish Massif), micritic seamounts (Rhenish Massif, Poland), pelagic outer shelf carbonate platforms (southern Morocco) and ramps (Montagne Noire, Moroccan Meseta) to micritic inter-reefal and arenitic, hemipelagic, peri-reefal areas (NW Australia). Individual taxa, however, were much more facies sensitive which may reflect different feeding behaviour. *Acrimeroceras* was widely distributed ("eudemic" [J.H. CALLOMON, 1985]) on the Tafilalt Platform of southern Morocco but was lacking in the basinal facies of the adjacent Maider Basin where contemporaneous beds yielded only low-diverse early sporadoceratids.

The presence of internal shell thickenings suggests that protection against shell-breaking predators, such as benthic arthropods, was important and indicates that contact with the seafloor occurred. This is supported by the sub-convex apertures and growth lines with only weak adult ocular flank sinus, similar as in *Nautilus*. Restriction of constrictions to dorsolateral whorl parts in *Acri. stella* n. sp. shows that the weakly curved inner flanks needed more strengthening than other whorl parts. The ventral interruption of varices reflects the fact that the keel stiffened the shell anyway. The decoupling of apertural (growth line) and mould constriction courses and their variability, as in *Cheiloceras* (*Cheiloceras*) and in *Oxytornoceras signatum* BECKER (see R.T. BECKER, 1993a), suggests that shell thickenings were secreted behind the apertural margin. The soft body was obviously able to contract and hide behind internal shell ridges. Since the wrinkle layer expands only slightly (ca. 20°, MB.C.2862) beyond the aperture on the preceding whorl, the animal stretched only a little out of its shell. Repaired shell breakages (MB.C.2865, Text-Fig. 11.11) between constrictions give evidence of survived arthropod attacks.

A range of still undescribed intermediates from the Canning Basin and well-dated faunal sequences demonstrate that thinly oxyconic *Acrimeroceras* were derived from thicker and late oxyconic *Paratornoceras* which again split off in the *rhomboidea* conodont zone from early dimeroceratids with still rounded venter (*Praemeroceras*, see R.T. BECKER, 1993a). *Praem. primaevum* (SCHINDEWOLF) is a species that both in the course of sutures and in time (R.T. BECKER & M.R. HOUSE, 1997) is intermediate between oldest Paratornoceratinae and *Praem. petterae* (PETERSEN), the oldest member of the Dimeroceratinae. Details of the phylogeny and taxonomy of the whole group will be published elsewhere but it is significant that hypermorphotic (R.T. BECKER, 1986) and indeterminate (based on unpublished Moroccan "megaconchs") shell growth occurred already in *Praemeroceras* which, however, still has longidomic and slowly expanding whorls. The gradual change from longidomic, discoidal praemeroceratids to slightly mesodomic and oxyconic paratornoceratines reflects a change from demersal to pelagic, vertically migrant (migronectonic [R.T. BECKER, 1996]) lifestyle at the base of UD II-F (within the Upper *rhomboidea* Zone). Interestingly, globally no other oxyconic ammonoid group is known from the

same time. *Oxytornoceras* and the *Cheil.* (*Raymondiceras*) *praelentiforme* Group died out with the Upper Condroz Event late in UD II-E (Lower *rhomboidea* Zone). The Australian sections show that there was no overlap of *Oxytornoceras* and earliest *Paratornoceras* in rich successive faunal assemblages. It seems that adaptive radiation of Dimeroceratidae into pelagic habitats was only possible after the "niche" for oxyconic cephalopods was freed from competitors. The distribution of oxyconic ammonoids in space and time seems to allow general conclusions concerning competition and the availability and restrictions of "synecological licences" in extinct cephalopods.

The extremely compressed, more lanceolate, ribbed and larger *Acri. stella* n. sp. is morphologically more advanced and specialized than the succeeding, younger *Acri. falciculatum*. This suggests that no phylogenetic sequence or chronomorphocline is preserved at Dar Kaoua but that both are allopatric immigrants into the Tafilalet Platform area. For unknown ecological reason, paratornoceratin retreating soon after the deposition of the two investigated beds or became at least very rare. A single extremely compressed *Polonites* n. sp. (MB.C.2873), resembling the Polish and German representatives, but of unknown age, indicates that further populations of the subfamily spread to Morocco at a later stage in its evolution. The revision of relatives from Europe and Australia will allow a more precise reconstruction of evolutionary and migrational patterns.

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