

Morphometry and Taxonomy of Lower Famennian Sporadoceratidae (Goniatitida) from Southern Morocco

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14 Text-Figures and 2 Plates

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Morphometrie und Taxonomie von Sporadoceratidae (Goniatitida) aus dem Unteren Famennium von Südmarokko

Zusammenfassung

Die Sporadoceratidae gehören zu den am weitesten verbreiteten und langlebigsten Goniatiten-Familien des Devon, jedoch sind viele zugehörige Taxa nur unzureichend bekannt. Eine kritische Literatur-Durchsicht und neue Funde zeigen, dass künftig eine Reihe von neuen Gattungen zu unterscheiden sein wird, die iterativ Spiralstreifung und offennabelige Gehäuse hervorbrachten. Die ursprünglichste Gattung, *Maeneceras*, hatte ihre Blütephase im Oberdevon II (UD II) und nur seltene Vertreter reichten bis ins obere Famennium (UD V). *Goniatites biferus* PHILLIPS (1841) wird als subjektives Synonym zu *Goniatites ungeri* MÜNSTER (1840) aufgefasst, sodass die *Maene. biferum*-Zone (UD II-G) in *Maene. subvaricatum*-Zone umzubenennen ist. Die morphometrische Analyse einer Population aus dem unteren Famennium (UD II-G) von Hassi Nebech (S-Tafilalt, Marokko) wird genutzt, um exemplarisch die Bedeutung von Schalen- und Suture-Merkmalen sowie die intraspezifische Variabilität in der Gruppe zu erfassen. Ergebnisse werden zur Revision des Artbestandes genutzt. Es bestätigte sich, dass innere Schalenverdickungen starken ontogenetischen Wandlungen unterworfen sind und bei *Maeneceras* nicht zur einfachen Artunterscheidung taugen. Das Schalenwachstum war nicht terminiert, sondern erfolgte zeitlebens. Eine Analyse der A₂-Lobentiefe zeigte, dass drei Morphotypen unterschieden werden können; jedoch existierte in der untersuchten Fauna keine scharfe Arttrennung, wie sie in jüngeren Schichten klar gegeben ist. Dies beruht entweder auf zu starker Kondensation und Mischung verschieden alter Formen, oder die Population dokumentiert einen Fall begonnener, aber noch nicht vollzogener Artbildung.

Abstract

The Sporadoceratidae are amongst the most widespread and longest-ranging ammonoid families of the Devonian. However, many forms are still poorly known. A critical review of literature and new records indicate that a range of new genera should be distinguished, based on the iterative introduction of spiral ornament and open umbilicate whorls. The oldest genus, *Maeneceras*, had its acme in Upper Devonian II (UD II) but rare members ranged into the upper Famennian (UD V). *Goniatites biferus* PHILLIPS (1841) is regarded as a subjective synonym of *Goniatites ungeri* MÜNSTER (1840). Therefore, the *Maene. biferum* Zone (UD II-G) has to be renamed as *Maene. subvaricatum* Zone. The morphometric analysis of a population from the lower Famennian (UD II-G) of Hassi Nebech (S-Tafilalt, Morocco) is used as a case study to evaluate the significance of shell and sutural features as well as the intraspecific variability in the group. Results are used for taxonomic revisions.

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Internal shell thickenings change throughout ontogeny and cannot be used easily to distinguish species in *Maeneceras*. Growth of the conchs continued throughout life without reaching a fixed maximum size. An analysis of the depths of A_2 lobes showed the presence of three morphotypes but there was no clear species separation as known from younger strata. This is either based on too strong condensation and mixture of individuals of different geological age, or the population documents a case of initial but not yet completed speciation.

1. Introduction

The Sporadoceratidae are one of the most successful goniatite families of the Upper Devonian and it ranged from the base of the Upper Nehden-Stufe (Upper Devonian = UD II-G) up to the level of the global Hangenberg Event near the Devonian/Carboniferous boundary or even into the hypoxic event beds (UD VI-E; M.R. HOUSE et al. [1986]: specimens recorded from the Bedford Shale). This gives a lifespan of ca. 70 % of the Famennian which may equal 7–10 ma. Only the Tornoceratidae have a longer Upper Devonian range. In tropical/subtropical regions, the family was cosmopolitan. Records (Text-Fig. 1) come from North America (Ohio, Pennsylvania, New York, Oklahoma), South America (Bolivia), North Africa (northern and southern Morocco, southern Algeria), southern Europe (SW Spain, Cantabrian Mts., Montagne Noire, Pyrenees), Middle Europe (Rhenish Massif, Harz Mts., Thuringia, Franconia, Saxony, SW England, Armorican Massif, Carnic Alps), eastern Europe (Holy Cross Mts., Silesia, Moravia, Lublin Basin), Russia (Bashkiria, S Urals, SE Urals, Taimyr), Asia (Iran, Kazakhstan, Kirgisia, Turkestan, Inner Mongolia, South China) and Australia (Canning Basin, New South Wales). A total of eightyfive species and subspecies has been named but most of these are inadequately known and currently it is difficult to decide which of these should be accepted as valid and which should be treated as subjective synonyms. Other forms clearly representing distinctive taxa have only been mentioned in open nomenclature (e.g., O.H. SCHINDEWOLF, 1937 and R.T. BECKER et al., 1999).

As illustrated by R.T. BECKER (1993a), *Maeneceras nuntio*, the oldest member of the genus, originated from advanced cheiloceratids, such as *Cheil. (Puncticeras) lagowiense* (GÜRICH), by the insertion of shallow lobes in the ventral saddle (A_2 lobes) and by small lobes (U lobes) in the internal saddle. At the same time, maximum conch sizes increased, probably by the hypermorphotic addition of whorls. Subsequently in the early evolution of the group (Text-Fig. 2), the rounded A_2 lobes became gradually deeper, leading to end-members such as *Maene. acutolaterale* with an A_2 that is as deep as the A_1 . Some middle to upper Famennian relatives kept small and shallow A_2 lobes but can be distinguished by spiral ornament, as is more characteristic in Carboniferous goniatites. Yet other, still undescribed, lower Famennian forms changed to slowly expanding and open umbilicate shells, or, in the endemic *Iranoceras*, the dorsal lobes remained very shallow. Diversification in the family was reached either by the introduction of more complexity in sutures and shell features, or by a return to characters known from ancestral Cheiloceratidae which had declined parallel with the rise of oldest sporadoceratids.

Taxonomic revisions as a foundation for a better phylogenetic understanding are mostly hindered by the lack of knowledge concerning the significance of morphological features and of intraspecific variabilities. As a general fact in the Devonian, hardly any ammonoid populations have been studied statistically and by detailed morphometry. A large assemblage of almost 300 well preserved

maeneceratids collected from a single nodular limestone bed in southern Morocco is used here as a case study to investigate intraspecific variabilities, with special emphasis on shell parameters, internal shell thickenings, and on the size/depth of sutural elements. The question of chromomorphoclines in evolution versus true speciation will be addressed.

Abbreviations

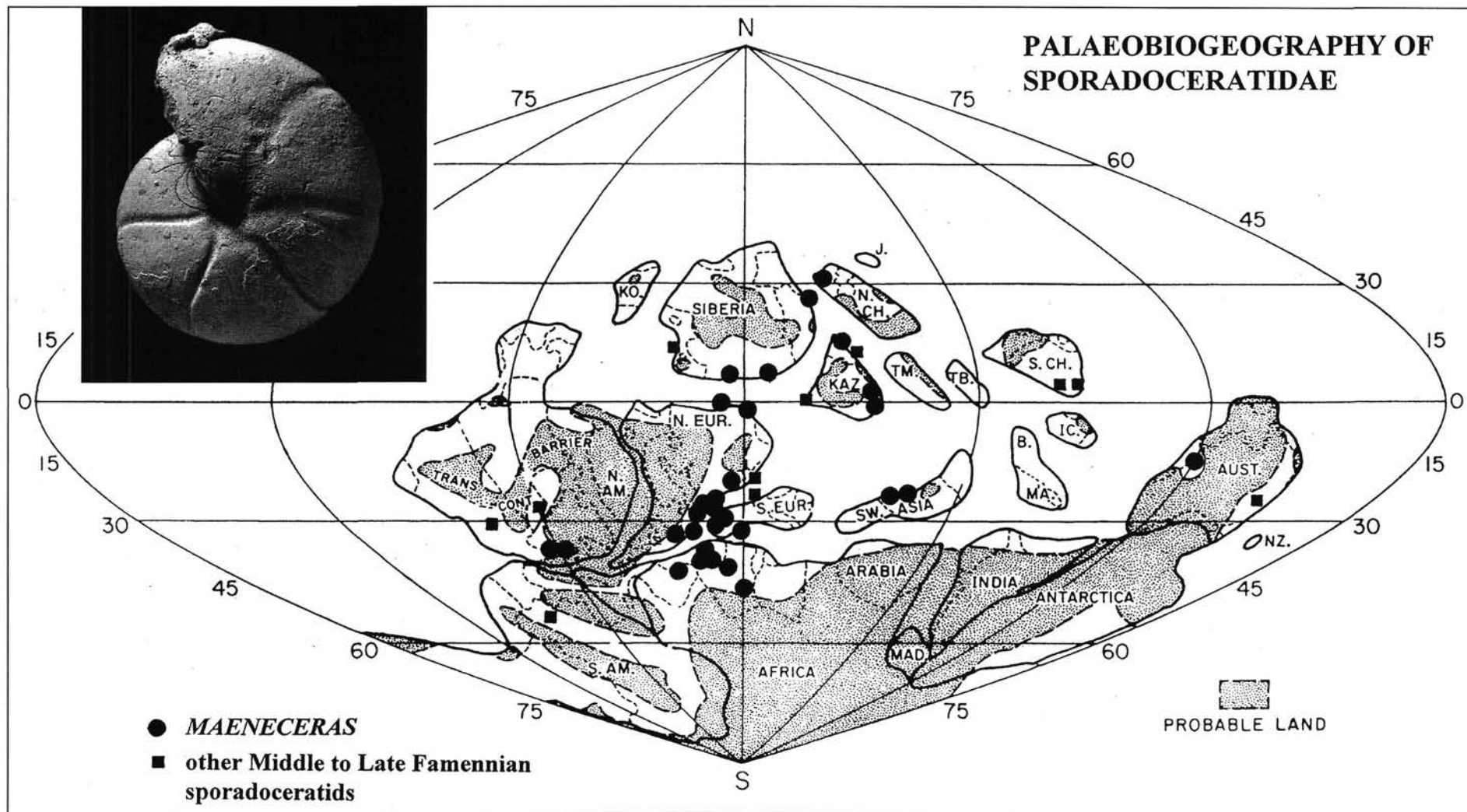
E = ventral or external lobe; A = adventitious flank lobe; Le = outer (subumbilical) lateral lobe; Li = inner lateral lobe; I = dorsal or internal lobe; d = diameter; ww = whorl widths; wh = whorl height; ah = apertural height; uw = umbilical widths.

Upper Devonian ammonoid zone abbreviations follow R.T. BECKER (1993b). BSHGP = Bayrische Staatssammlung für Historische Geologie und Paläontologie. MB.C. = cephalopod collection of the Museum für Naturkunde, Berlin. GPIG = Geologisch-Paläontologisches Institut Göttingen.

2. Locality and Methods

The Tafilalt and Maider of southern Morocco (Anti-Atlas) provide ideal conditions to obtain large Devonian ammonoid populations from single beds. Either selected goniatite-rich condensed cephalopod limestones or deeply weathered haematitic shale units are suitable for the analyses of assemblages. R.T. BECKER (1993a) studied intensively the stratigraphy, ammonoid faunas and facies development of the early Famennian (Nehdenian, UD II) in the Anti-Atlas and drew attention to the wide distribution of marker limestones of the basal UD II-G (Lower *marginifera* Zone) with common earliest sporadoceratids. This unit transgresses over a widespread unconformity in the middle of Upper Devonian II and contains a sequence of beds, some of which are rich in paratornoceratines (see V. EBBIGHAUSEN et al., this vol.). In the best described successions, e.g., at Jebel Amelane and Hamar Laghdad, there seems to be a sequence of maeneceratids from forms with very shallow to forms with moderately deep A_2 lobes. However, due to the limited extraction of specimens from very solid limestone, this is currently based on rather small collections. In any case, beds currently assigned to the *Maene. biferum* Zone can be subdivided by the presence or absence of abundant *Acrimeroceras*, with the *Acrimeroceras* Bed(s) forming the lower part of UD II-G. This is supported independently by a rough description of the Famennian at Ouidane Chebbi in the eastern Tafilalt by Z. BELKA et al. (1999).

Due to the marly facies development in more basinal setting, the best locality to obtain large early sporadoceratid faunas was found in the Hassi Nebech area, in the southern Tafilalt Basin. The investigated locality (Text-Fig. 3) has not yet been mentioned in the vast literature on the Anti-Atlas but it is rather close (ca. 3 km W) to the late Givetian and Frasnian Hassi Nebech sections described by M. BENSaid (1974) and M. BENSaid et al. (1985). At the western end of the Hassi Nebech Devonian belt, faulted and partly repeated Famennian limestones are exposed in low ridges a few hundred meters SE of the track which turns northwards around the rough south-



Text-Fig. 1.

Palaeobiogeographic distribution of *Maeneceras* (black dots) and of other middle to late Famennian Sporadoceratidae (black squares).

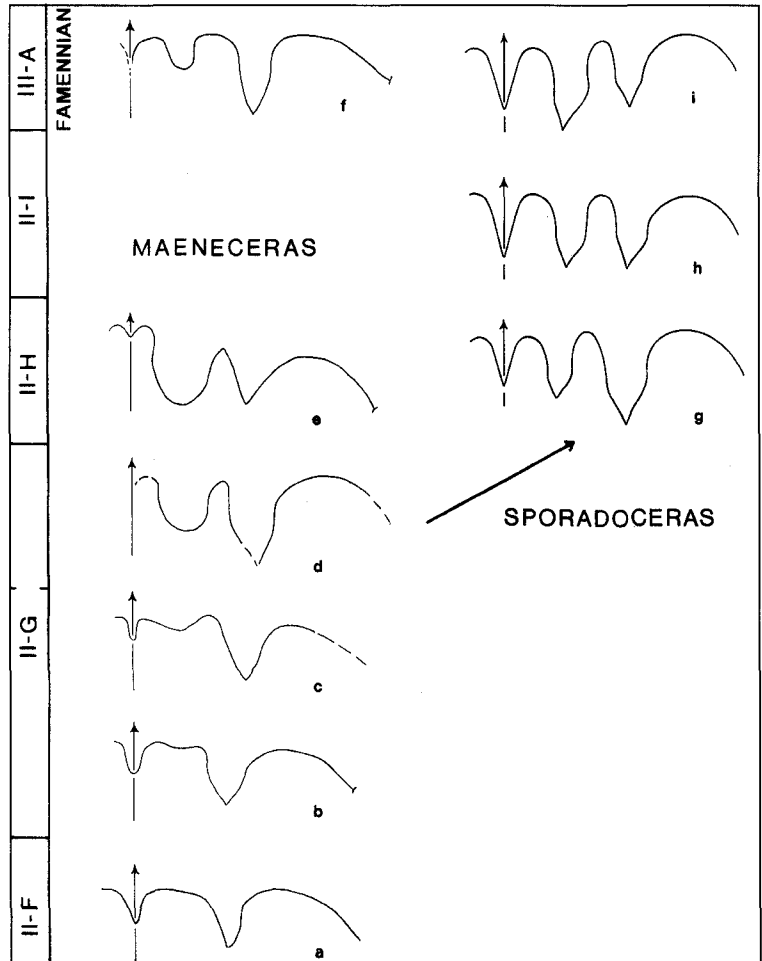
S. AM. = South America; N. AM. = North America; N. EUR. = Northern Europe; S. EUR. = Southern Europe; KAZ. = Kazakhstan; KO. = Kolyma, eastern Siberia; TM. = Tarim Basin; TB. = Tibet; N. CH. = North China; J. = Japan; S. CH. = South China; B. = Burma; MA. = Malaysia; IC. = Indochina Block; NZ. = New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

Migrations and faunal exchanges occurred along the Prototethys, the Urals seaway, through a central Asian route (Kazakhstan – North China), via the Afro-Appalachian link, and from eastern North America southwards (to Bolivia). The illustrated *Maene. subvaricatum subvaricatum* (SOBOLEV) is MB.C.2883 (= No. 271) from Hassi Nebech (S. Morocco).

Text-Fig. 2.

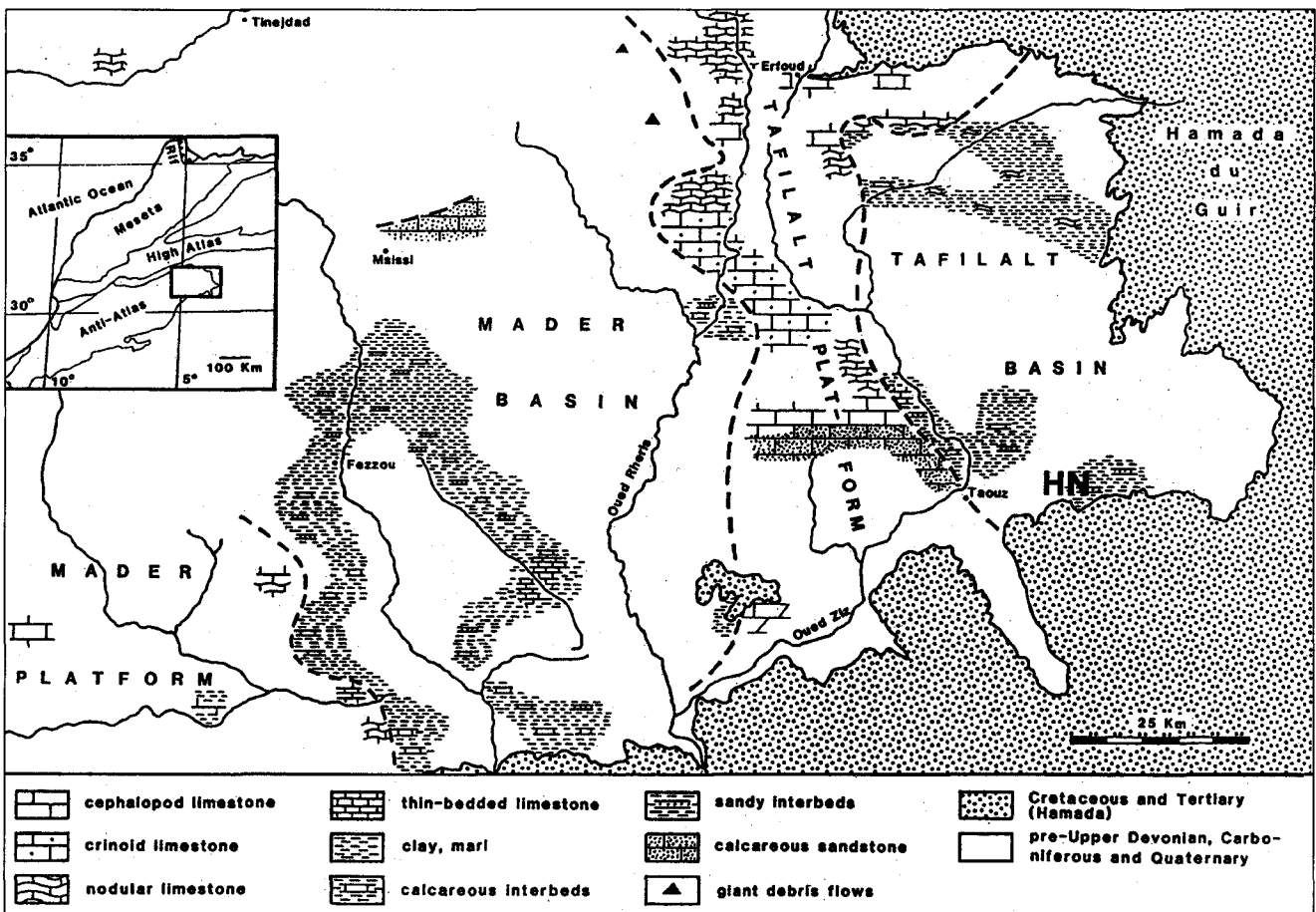
Gradual deepening of the second adventitious lobe in lower Famennian *Maeneceras* phylogeny, origination of *Sporadoceras* by the appearance of pointed A_2 lobes, and maintenance of small A_2 lobes in some middle Famennian forms.

a = *Cheil. (Puncti.) lagowiense*; b = *Maene. subvaricatum nuntio*; c = *Maene. subvaricatum subvaricatum*; d = *Maene. latilobatum*; e = *Maene. acutolaterale*; f = ?*Maene. rotundum*; g = *Sporad. teichertii*; h = *Sporad. bilanceolatum*; i = *Sporad. angustisellatum*. Sutures are based on M.S. PETERSEN (1975) and R.T. BECKER (1993a). Species are arranged according to their oldest appearances in Upper Devonian II-F to III-A.



Text-Fig. 3.

Early Famennian palaeogeography of the eastern Anti-Atlas (after J. WENDT, 1988: Text-Fig. 1) and the position of the investigated Hassi Nebech section (HN) in the southern Tafilalt Basin.



Text-Fig. 4.

Sketch of a suture of *Maene. subvaricatum subvaricatum* illustrating the measurements of A_1 and A_2 lobe depths (4a), in comparison with sutures of a syntype of *Gon. ungeri* (4b, BSHGP VII 890; see R.T. BECKER, 1992, Text-Text-Fig. 3b), the lectotype of *Gon. biferus* (4c, IGS 57301), and of an *Erfoudites ungeri rotundolobatus* from Mrakib (Maider, 4d, MB.C.2882).

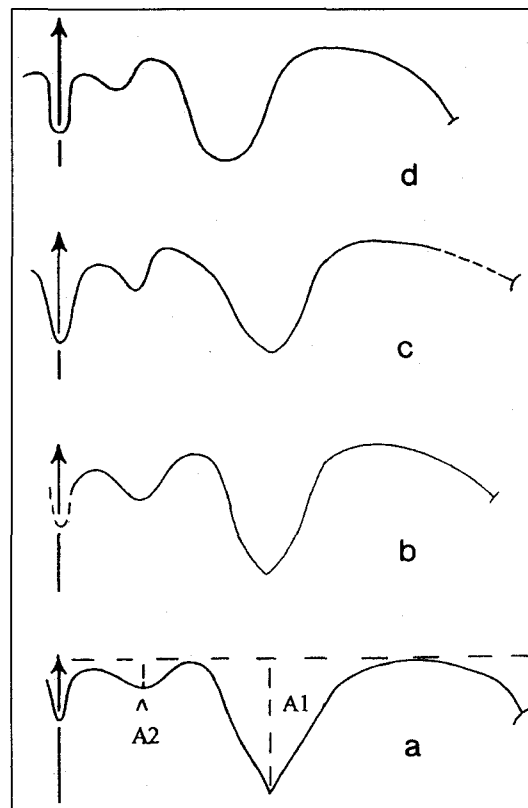
eastern foot of Jebel Begaa. A collection of ca. 300 maeneceratids was excavated by VE and JB from yellow to slightly reddish weathering marls with limestone nodules. The aragonitic shells have mostly been dissolved but the majority of moulds are complete and show nicely internal shell thickenings and sutures. Phragmocones are often filled by coarse white sparite. Associated faunal elements are orthocones, some bivalves, and other goniatites, such as *Armatites planidorsatus* (MÜNSTER) and *Falcitornoceras aff. bilobatum* (WEDEKIND). To the south, an important undescribed middle Famennian micritic succession follows which has the only rich Upper Devonian III goniatite and clymenid faunas of the whole Tafilalt, followed by *Annulata* Event beds with abundant platyclymenids and by fossiliferous higher levels of UD IV. Only a few hundred meters further to the S, Carboniferous sandstones and quartzites form a steep cliff.

All measurements of shell parameters were obtained with a digital slide rule. In each specimen the number of varices (mould constrictions) was counted, but a distinction between complete (from umbilicus to umbilicus: "forma sulcifera") and incomplete course (thinning from the venter on to the outer flanks: "forma subvaricata") was kept. Forms lacking constrictions are assigned to the morphotype "forma bifer"; this terminology utilizes a subspecies distinction outlined by J. KULLMANN (1960). The comparison of the depths of the two adventitious lobes (Text-Fig. 4a) is based on measurements from a radial line touching the top of the A_1 - A_2 -saddle. Since the outer (A_2 -E) saddle is often lower than the inner (A_1 - A_2) ventral saddle, it is important not to measure the depths of A_2 from a line connecting the top of the two outer flank saddles. The difference between the height of both ventral saddles has not been measured systematically but seems of little significance in the studied assemblage. However, it is a feature that has been used by former authors to distinguish taxa such as *Maene. lagowiense* GÜRICH and *Maene. descendens* (SCHMIDT) and undescribed Australian faunas rarely include a new form (*Maeneceratid* n.sp.) with elevated outer ventral saddle.

3. Phylogeny of the Sporadoceratidae

A critical evaluation of Moroccan faunas requires some review and comments on the overall taxonomy and iterative phylogeny of the Sporadoceratidae. There are several new genera and species from higher parts of the Famennian which will be briefly mentioned in open nomenclature but descriptions of these will be given elsewhere.

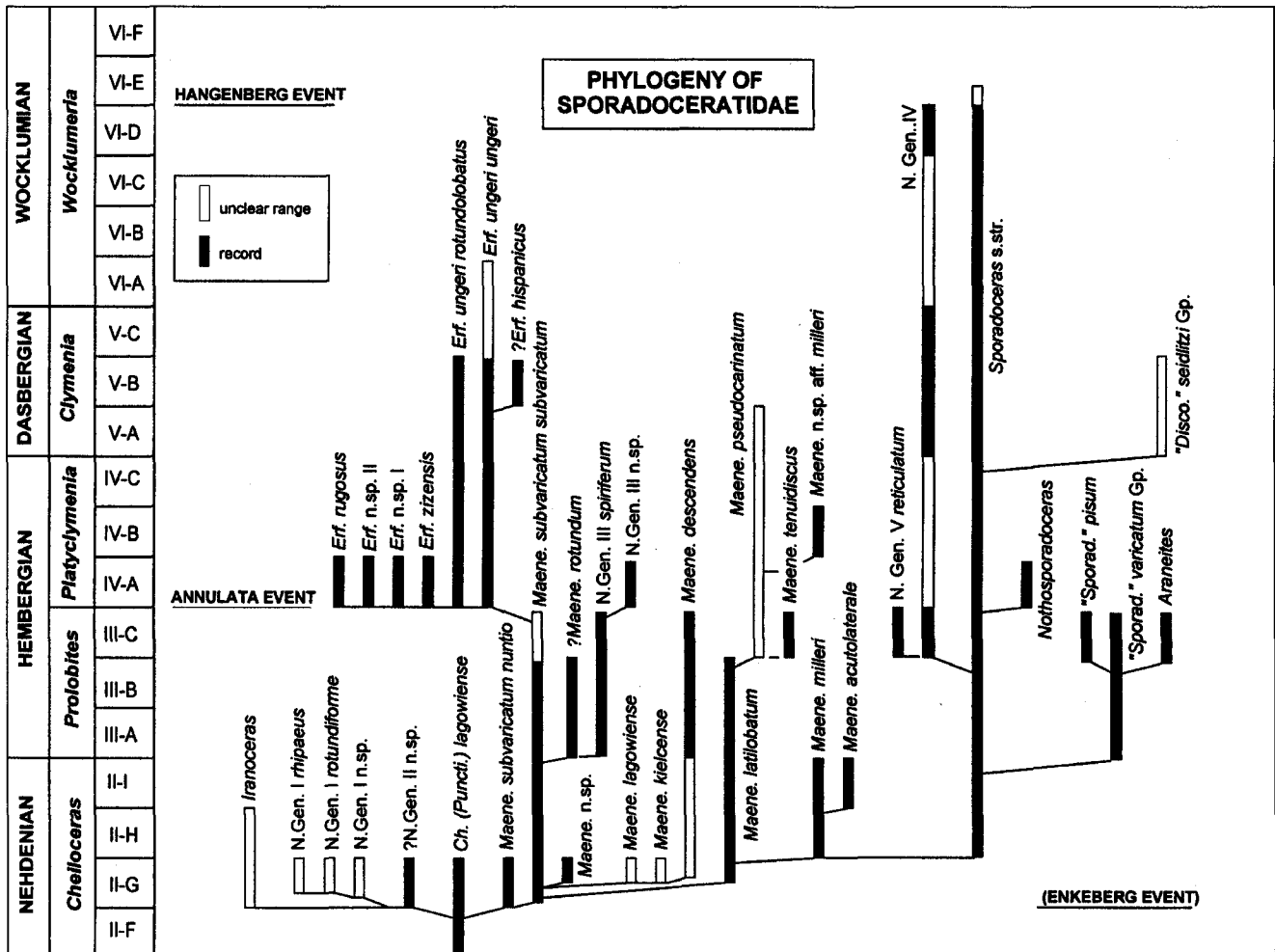
Following the last revision of R.T. BECKER (1993a), all sporadoceratids with deep dorsal and rounded A_2 lobes are assigned to *Maeneceratid* HYATT. The genus is supposed to range from the base of UD II-G (Lower *marginifera* Zone) to ca. the middle part of UD V (*expansa* Zone, Dasbergian). The typical group with shallow to very deep A_2 is cosmopolitan (Text-Fig. 1) in the upper part of the Nehdenian (UD II) and includes the advanced type-species, *Maene. acutolaterale* (SANDBERGER & SANDBERGER) with extensive A_2 that is as deep as A_1 (Text-Fig. 2e). The supposedly best known, most widespread and most often quoted early species is *Maene. biferum* (PHILLIPS) which is said to include several subspecies. *Iranoceras* WALLISER has very shallow dorsal and A_2 lobes as in most primitive maeneceratids (*Maene. biferum nuntio* BECKER). It probably split off from *Cheil.* (*Puncticeras*) as a parallel lineage or sister group (Text-Fig. 5). The type-species, *Sporad. (Iran.) pachydiscus* WALLISER (1966), is a homonym of *Sporad. pachydiscus* SCHINDEWOLF (1921: p. 151), which, however, remained an invalid nomen nudum. SCHINDEWOLF's type specimen from UD V of Wildungen was



never illustrated or described. A specimen (No. 5735) collected and identified by SCHINDEWOLF as *Sporad. pachydiscus* from Schübelhammer (Franconia) in the collection of the former Prussian Geological Survey (now in Berlin-Spandau) is conspecific with *Sporad. orbiculare* (MÜNSTER).

Still poorly documented is a new early Famennian second sister genus (N. Gen. I) of *Maeneceratid* with open umbilicus and slowly expanding whorls. It includes a new species from southern Morocco, *Sporadoceras rotundiforme* BOGOSLOVSKIY, and perhaps *Lagowites rhipaeus* BOGOSLOVSKIY. The new genus is obviously exceedingly rare in the Tafilalt and no representative was found at Hassi Nebech. A similar evolutionary trend led in UD IV from *Sporadoceras* to the open umbilicate endemic *Nothosporadoceras* BOGOSLOVSKIY of the southern Urals and Kazakhstan. Further studies are needed to clarify the taxonomic position of Moroccan UD II-G maeneceratids with evolute and depressed inner whorls; these possibly represent a third group (?N. Gen. II) of the initial radiation phase. So far, it has only been found in more basinal, haematitic (hypoxic) facies of the Tafilalt Basin and of the Maider. The introduction of evolute early stages in sporadoceratid evolution can be seen as an iteration to earlier identical conch changes from *Cheiloceras* (*Raymondiceras*) to *Cheiloceras* (*Cheiloceras*). The same trend was later repeated in the middle Famennian (UD III) "*Sporad.*" *varicatum* Group (see R.T. BECKER et al., 1999) which probably gave rise to the keeled *Araneites* BOGOSLOVSKIY and to the strange "*Sporad.*" *pisum* NALIVKINA.

The overall majority of middle (UD III/IV) and late (UD V) Famennian supposed *Maeneceratid*



Text-Fig. 5.

Current knowledge of stratigraphical ranges and of the phylogenetic relationships of Famennian Sporadoceratidae.

Two radiation episodes correlate with the global transgressive pulses of the Enkeberg and Annulata Events. Based on coiling (involute, convolute, evolute at early stages), keels (*Araneites*), the presence of a shallow A_3 (N. Gen. V, "*Disco.*" *seidlitzii* Gp.), the shape of dorsal sutures (*Iranoceras*), and on the presence (*Erfoudites*, N. Gen. III and IV) or absence of spiral ornament, a dozen generic groups can be distinguished in the family.

(sensu R.T. BECKER, 1993a) have kept a small A_2 , suggesting that less advanced species survived and diversified whilst the taxa with deep A_2 declined near the end of the Nehdenian. Exceptions from this rule are *Maene. latilobatum* (SCHINDEWOLF) from UD III-B and *Maene. tenuidiscus* (SCHINDEWOLF) from UD III-C of Gattendorf (Franconia; O.H. SCHINDEWOLF [1923]) and of Taltitz (Saxony, G. FREYER, 1957), *Maene. pseudocarinatum* (PETTER) from UD III-V of the Saoura Valley (southern Algeria), a specimen assigned by H. SCHMIDT (1922) to *Maene. acutolaterale* from the UD V of Drewer, and *Maene. n. sp. aff. milleri* from UD IV-B of the Maider (R.T. BECKER et al., 1999). It must be emphasized that all these forms are rare.

The common middle to late Famennian maeneceratid relatives not only have small A_2 lobes but shelly material and well-preserved moulds all show delicate to strong spiral ornament. This always involute group has been assigned by D. KORN (1999) to a new genus *Erfoudites*. As in some *Iranoceras* (O.H. WALLISER, 1966), several members show a trend to reduce the pointed tip of A_1 leading to sutures with only well rounded flank lobes (Text-Fig. 4c). O.H. SCHINDEWOLF (1927) argued that a secondary loss of the pointed lobe tip seemed unlikely, and that such forms probably evolved from the much older *Cheilloceras pompeckji* WEDEKIND with deeply rounded flank lobe. However, occasional specimens with round A_1 on one flank and pointed A_1 on the opposite disprove SCHINDEWOLF's assumption

and indicate that not too much taxonomic weight should be put on this feature. *Erfoudites* includes at least *Erf. rheriensis* KORN, *Erf. zizensis* KORN (type-species), *Erf. rugosus* KORN, *Goniatites ungeri* MÜNSTER, *Sporad. spirale* WEDEKIND (= *Sporad. striatum* WEDEKIND, 1918, nom. nud.), *Sporad. tenuistriatum* BOGOSLOVSKIY, *Sporad. rotundolobatum* SCHINDEWOLF, *Praeglyphioceras moravicum* RZEHA, and two new species from the Annulata Event beds of the Rhenish Massif (Kattensiepen, n. sp. I) and of southern Morocco (Bine Jebilet, n. sp. II). Some of the taxa are most likely subjective synonyms.

Abundant material assigned to *Maene. spiriferum* (LANGE) (= *rotundum* var. *spiralis* LANGE nom. vad.) and to *Maene. aff. spiriferum* from the Mrakib (Maider; R.T. BECKER et al. [1999]) show evolute inner whorls. This suggests the distinction of a second sporadoceratid genus (N. Gen. III) with spiral ornament in UD III, with rare advanced species ("*Maene.*" n.sp. R.T. BECKER et al., 1999 from Mrakib) higher in UD IV. Iteratively, spiral lirae also appeared in advanced sporadoceratids with two deep and pointed A-lobes: N. Gen. IV *denticulatum* (PERNA) from the middle Famennian (UD III-C) of the Urals. Related forms occur in the upper Famennian of the Rhenish Massif and of Oklahoma but have not yet been described. The *denticulatum* Group may have given rise to "*Sporad.*" *reticulatum* NALIVKINA with a shallow third A-lobe which justifies to place the species in another new genus (N. Gen. V).

Rich and well preserved collections from Morocco show that all simple-lobed “maeneceratids of UD IV/V” have spiral ornament (see also Pl. 1, Figs. 1–2) but this may not be visible on corroded internal moulds. As suspected by R.T. BECKER (1992: p. 13), there is no evidence that true *Maeneceras* with small A_2 range so high. This implies that the only available mould (holotype) of *Sporad. hispanicum* KULLMANN from UD V of the Kantabrian Mts. should perhaps also be transferred to *Erfoudites*. Even more significant is the long overlooked fact that the lectotype of *Goniatites biferus* PHILLIPS (1841; see Text-Fig. 2 and Pl. 1, Figs. 3–4) from South Petherwin (Pl. 1, Figs. 3–4) comes from an area that has yielded rich ammonoid faunas over a long time, but, as outlined by B. F. SELWOOD (1960), no index ammonoid of strata older than UD IV (*Platyclymenia annulata* Zone) has been recorded. Not only seems the lectotype to be derived from UD IV/V beds, its sutures (Text-Fig. 4b) with small but rather narrow A_2 are also more similar to *Gon. ungeri* MÜNSTER (1832) (Text-Fig. 4a) than to the majority of UD II maeneceratids (for an exception, however, see Pl. 2, Fig. 9). The type is so badly preserved that preservation of spiral ornament cannot be expected. Despite this, *Gon. biferus* is regarded as a subjective younger synonym of *Gon. ungeri* (refigured on Pl. 1, Figs. 5–6), and the species name *biferus* should not be applied any more to UD II sporadoceratids and should not be used any more as the zonal index of UD II–G. In a similar way, *Sporad. subbilobatum* var. *meridionalis* FRECH from UD V of La Serre (Montagne Noire) probably falls in synonymy of *ungeri*. FRECH (1902: p. 81) himself raised the possible identity of his new species with *Gon. biferus*. As outlined below, the name *Maene. subvaricatum* (SOBOLEV) has to replace *biferus* in the lower Famennian.

Erfoudites is still rather common in middle Dasbergian (UD V–B) beds. S. LEWOWICKI (1959) reported “*Sporadoceras biferum*” from the lower Wocklum-Stufe (UD VI–A) of Dziko-wiec (Silesia). Such a young occurrence of potential *Erfoudites* has not yet been confirmed anywhere else in the world and should be verified by a restudy of Polish collections.

Another ambiguous species based on inadequately preserved material showing no ornament is *Sporad. rotun-*

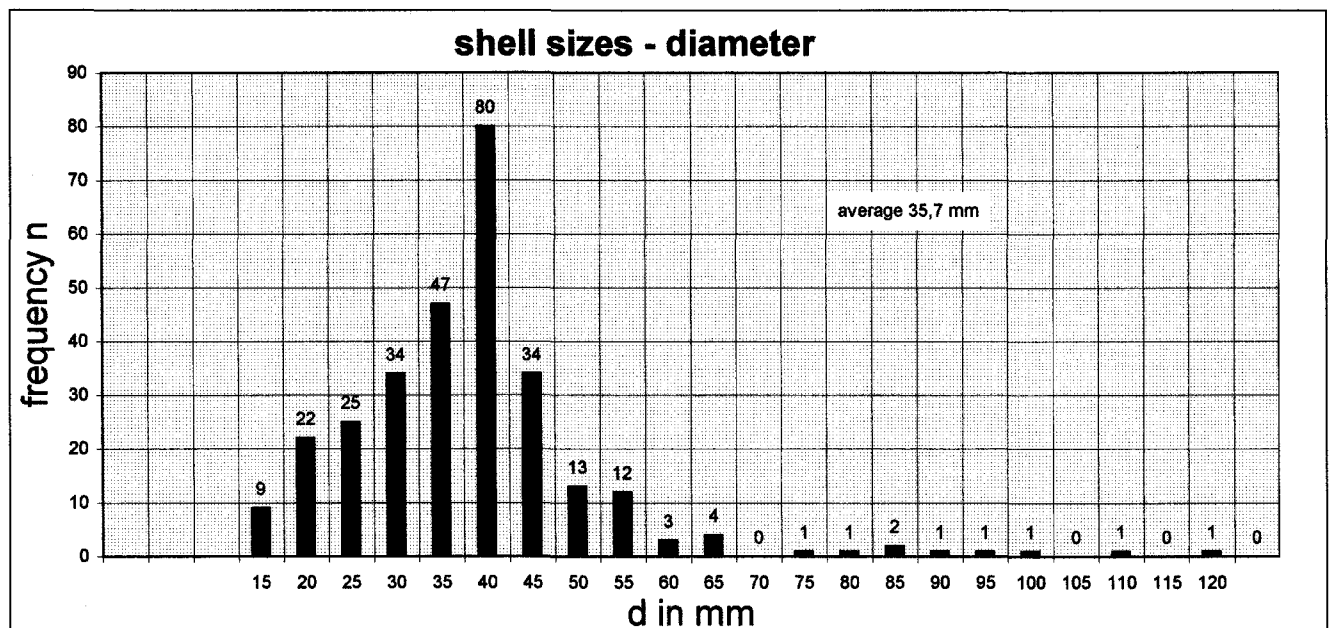
dum WEDEKIND from UD III of the famous Enkeberg. Its lectotype, designated by R.T. BECKER (1993a), is somewhat thicker than forms which were normally assigned to *biferum* (Text-Fig. 9) but the A_2 is more narrow (as in *ungeri*). The latter feature is not yet developed in UD II forms which have been included by previous authors in *rotundum* and which are present in the studied Hassi Nebech population (see later discussion). It is possible that W. LANGE’s (1929) distinction of *rotundum* and *rotundum* var. *spiriferum* is based on preservation only; LANGE himself (p. 44) confessed this possibility. This has to be clarified by a restudy of Enkeberg UD III sporadoceratids which is beyond the scope of this paper.

The same problem applies to some UD III forms assigned by authors to *Maene. biferum* (e.g., W. LANGE, 1929; A. FUHRMANN, 1954). *Lagowites* and the Praeglyphiocerati-dae were obviously derived from thick-shelled early *Maeneceras* (R.T. BECKER, 1993a).

4. Morphometry of the Hassi Nebech Population

4.1. Size Distribution

The Hassi Nebech population comes from very fine-grained, argillaceous, deeper-water lithofacies which excludes significant sorting and transport of goniatite shells by bottom currents. Conchs are not concentrated but irregularly distributed in the matrix of limestone concretions. The average size of specimens is ca. 35 mm in diameter but the largest goniatites are more than three times bigger (118.7 mm). Since some specimens of more than 100 mm diameter are still fully septate, and since the body chamber angle is near 360° (almost one whorl), sizes of almost 200 mm diameter must have been reached. This matches the largest known maeneceratids found at other Tafalalt localities (e.g., Bine Jebilet, R.T. BECKER, 1993a) but exceeds the maximum diameter estimated by R.T. BECKER (1986). From North America (New York State), M.R. HOUSE has also described a *Maeneceras* which still has sutures at $d = 117$ mm.



Text-Fig. 6. Histogram showing the asymmetric size distribution in the Hassi Nebech *Maeneceras* population suggesting indeterminate growth of some adults.

The size distribution resembles the pattern observed in contemporaneous Moroccan paratornoceratines (V. EB-BIGHAUSEN et al., this vol.). The shell size histogram shows an almost Gaussian distribution between 15 and 60 mm diameter. Size classes caused by synchronous mortality of differently aged partial populations, as recently documented in Middle Devonian goniatites (S. KLOFAK, 1999), are not present. However, there is a strong and gradual asymmetric extension towards large specimens. Mortality has been rather low in preserved juveniles and growths continued throughout life without reaching a pre-fixed maximum size. As in paratornoceratines, no change in septal spacing or of whorl expansion is seen in large specimens (see Pl. 2, Figs. 1–2) which would indicate either faster growth of some individuals or slowed growth at maturity. Mature shell modifications are unknown from all members of the family.

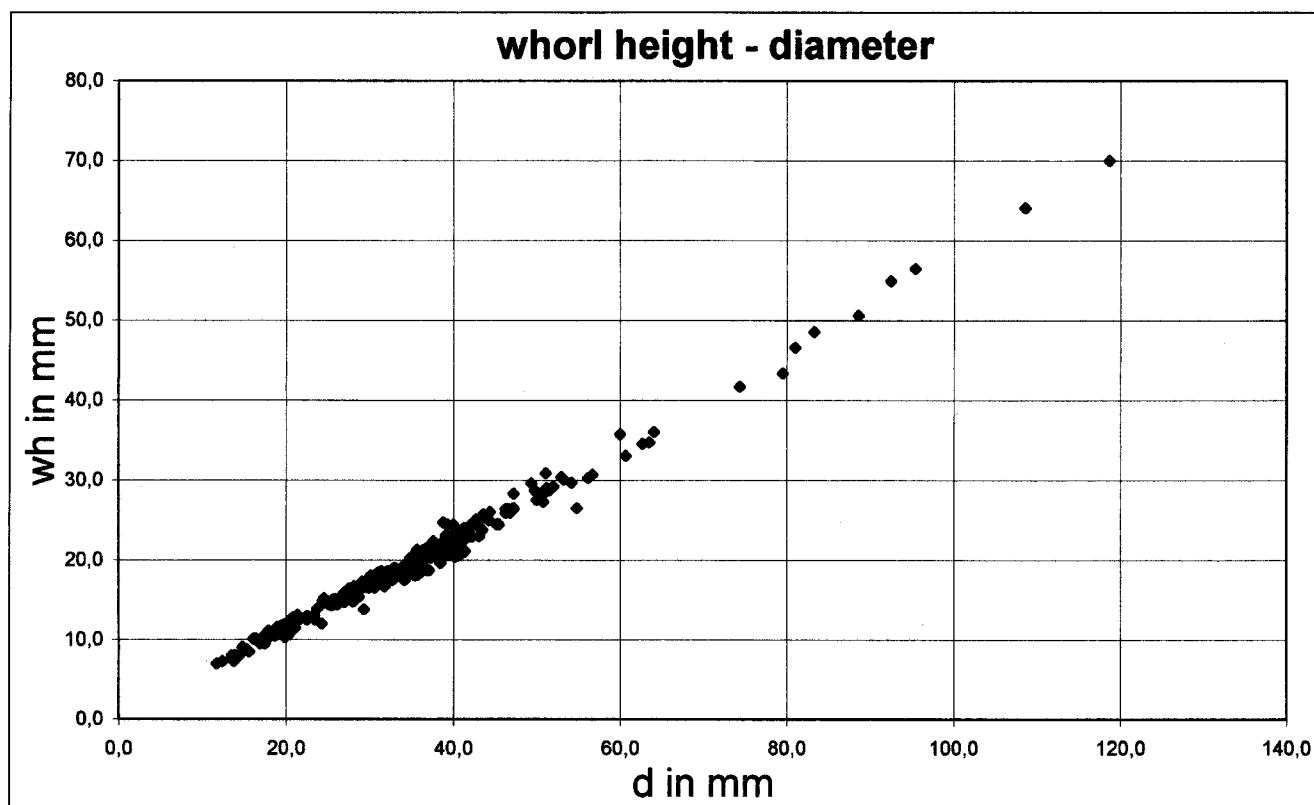
Ancestral cheiloceratids are considerably smaller than *Maeneceras* (R.T. BECKER, 1986) and hypermorphosis seems to have played a role during the evolutionary transition from members of one family to the next. The spread of large-sized early sporadoceratids and paratornoceratines coincided with the global transgression in the Lower *marginifera* Zone (R.T. BECKER, 1993b). This correlation does not support an observation of C. KLUG (1999) that size minima of goniatites coincided with global transgressive events. C. KLUG, however, recognized the appearance of large-sized ammonoids during the Upper Kellwasser and *Annulata* Events. Similarly, the giant gonio-clymenids of the Tafilalt come from a transgressive bed. However, giant crickitids occur in many regions of the world (North America, western Rhenish Massif, Montagne Noire, Australia) prior to the Upper Kellwasser level and in Morocco, the regressive *orbiculare* Bed has the largest diversity of large ammonoids (R.T. BECKER et al.,

1999). Current information indicates a strong local/regional facies influence on the distribution of large taxa and does not support a simple correlation between eustatics and maximum size.

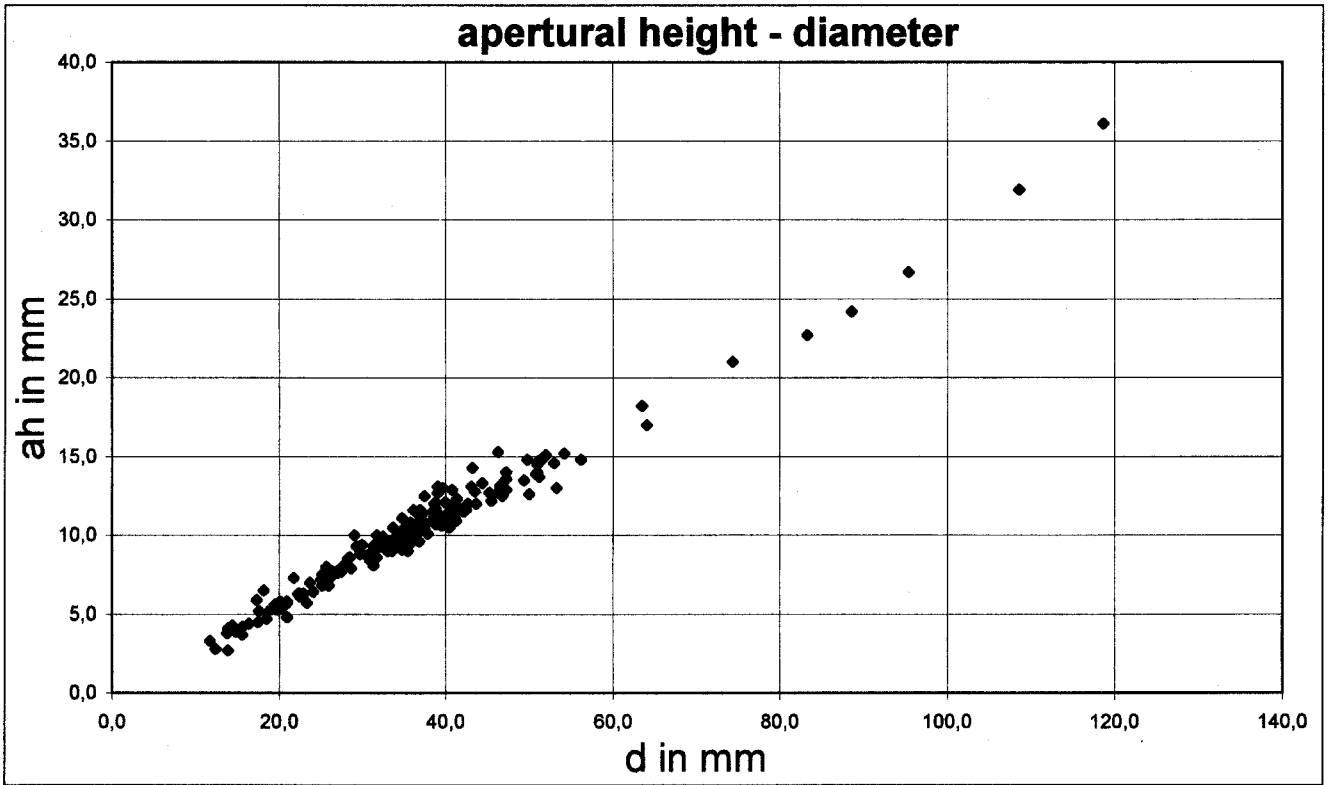
4.2. Shell Parameters

Shell parameters such as relative whorl height, apertural height, whorl widths and umbilical widths have been used in sporadoceratids to distinguish species. The morphometric analysis of the Hassi Nebech population gives clear indications of their variability within one time slice. Text-Fig. 7, for example, illustrates the rather restricted variability and ontogenetic constancy of the wh/d ratio, which in involute goniatites is a measure of whorl expansion. The umbilicus is very small in all specimens and was probably always closed by the shell. The average rate of wh/d lies around 56.5 % with a few specimens (ca. 6 %) exceeding 60 %, a value that is more typically reached in involute posttoroceratids.

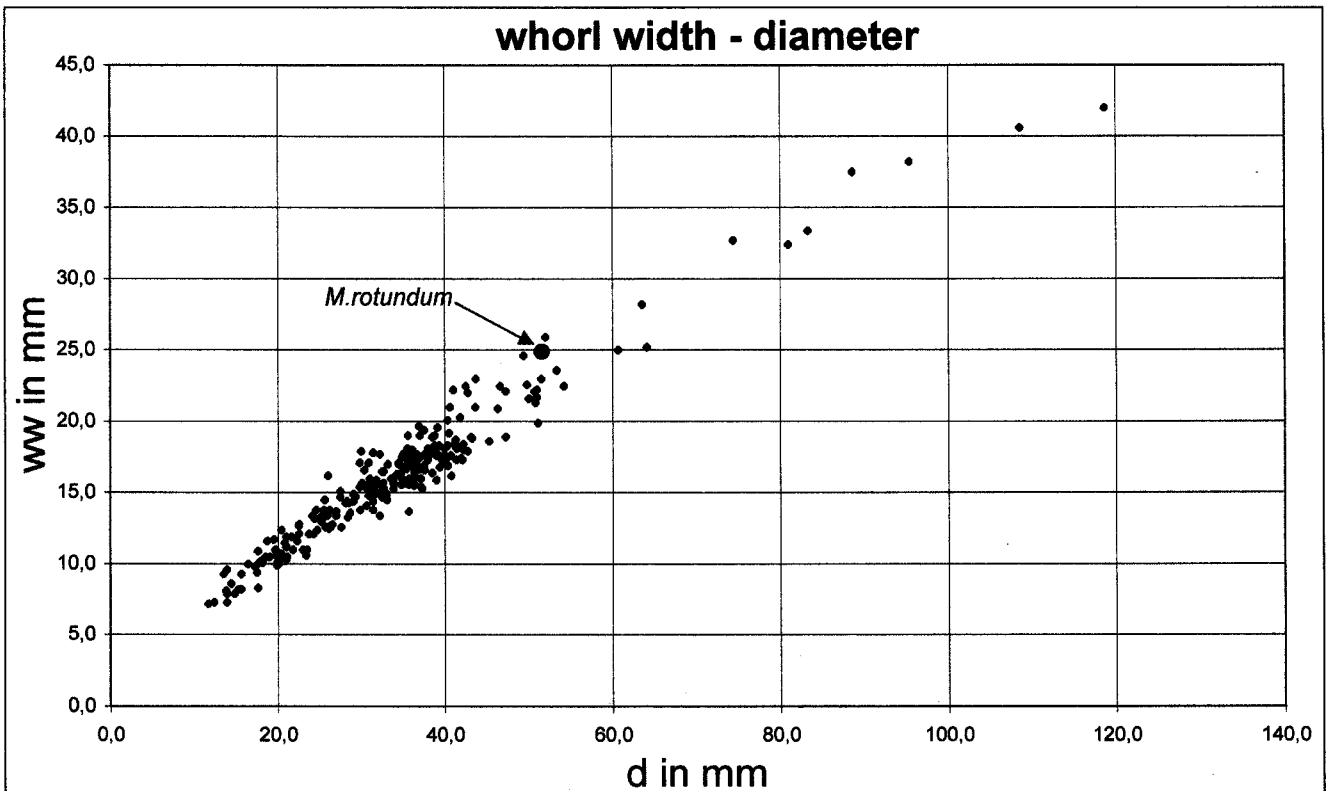
Significant variability in whorl expansion rates is shown by the ah/d ratios (Text-Fig. 8). Between ca. 20 and 50 mm diameter, there are some morphotypes with ah reaching more than 30 % diameter, but the average lies at 28.4 %. There are also some small slowly expanding specimens (ah around 20–22 % d) which tend to be rather thick. Such morphotypes are well visible in the whorl widths plot (Text-Fig. 9) and their field of variation reaches the value of the lectotype of *Maene. rotundum*. R.T. BECKER (1993a: Pl. 26, Figs. 7–8) has illustrated thick small morphotypes of *Maene. biferum nuntio* and indeed several of the thick morphs (e.g., MB.C.2875 = No. 240, Pl. 2, Figs. 3–4) share the very shallow A_2 and should be assigned to that taxon. In addition, there are some larger, rather thick specimens (e.g., MB.C.2876, Pl. 1,



Text-Fig. 7.
Restricted variability of the wh/d ratio in the ontogeny of Hassi Nebech maeneceratids.



Text-Fig. 8. Variability of the ah/d ratio in the ontogeny of Hassi Nebech maeneceratids showing a separation of more depressed and more slowly expanding morphotypes up to ca. 50 mm diameter.



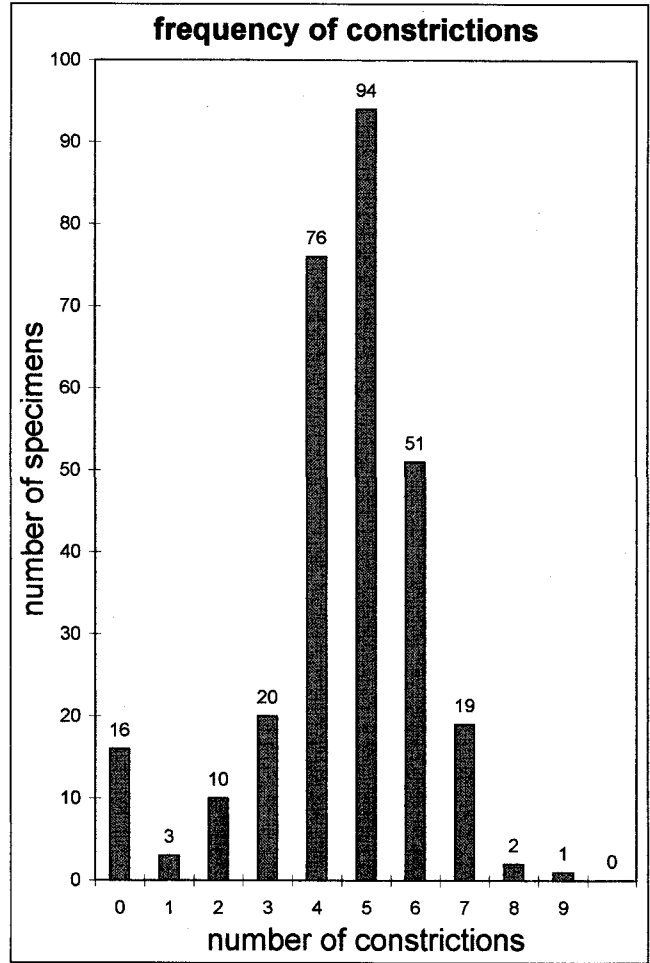
Text-Fig. 9. Variability of relative whorl widths in Hassi Nebech maeneceratids showing the presence of thicker and more compressed morphotypes up to 50 mm diameter. The lectotype of *Maene. rotundum* is plotted for comparison and falls in the field of thick morphotypes.

Text-Fig. 10.
Histogram showing the number of constrictions per whorl in Hassi Nebech *Maeneceras*.

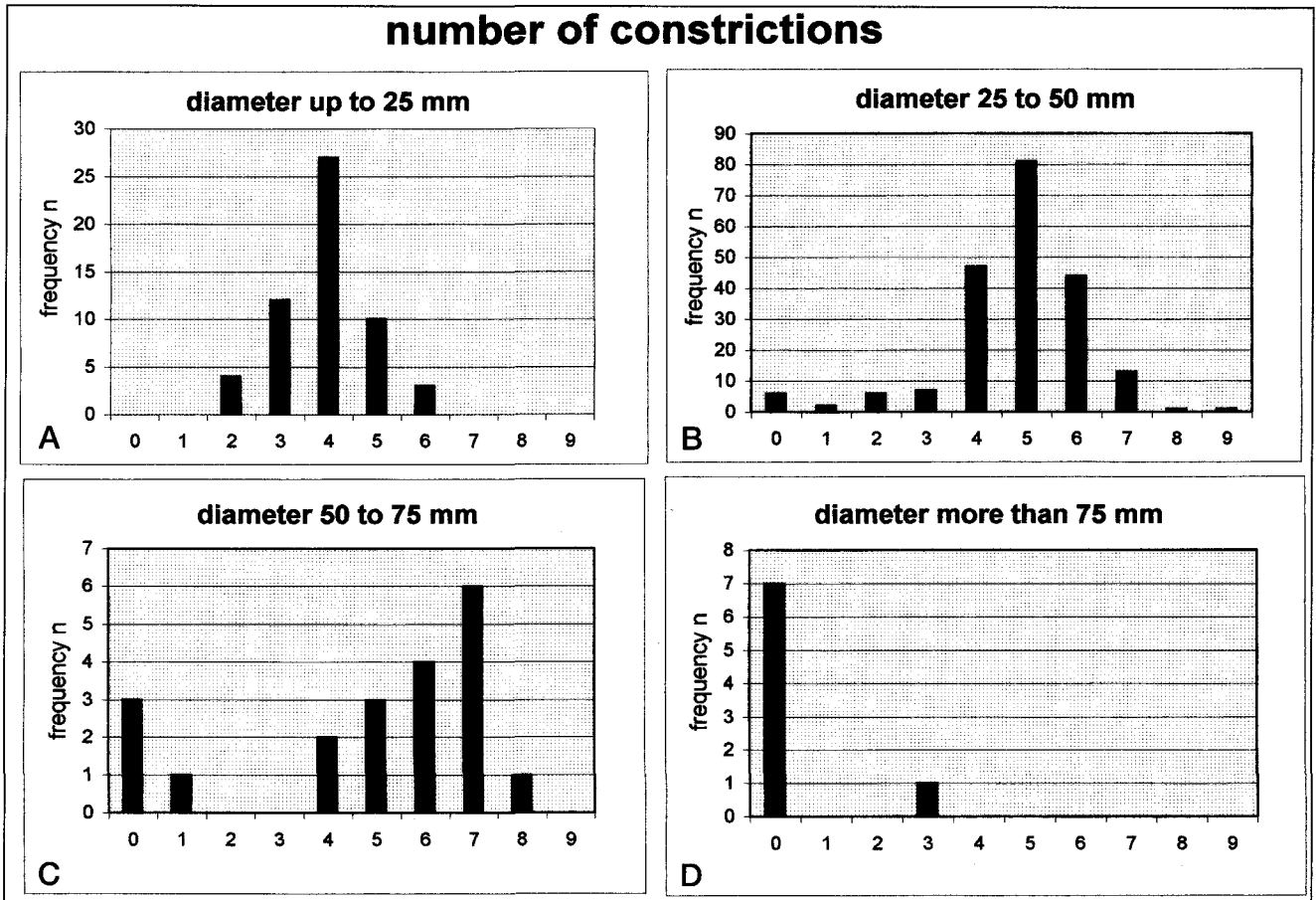
Figs. 13–14) with deeper A_2 . Since no clear separation of thin and thicker morphs is seen, no taxonomic distinction is made at Hassi Nebech based on ww/d ratios alone. However, it cannot be excluded that both forms can be better distinguished in assemblages of other localities/regions or in younger (UD III) faunas. A similar pair of thin and thicker forms seems to occur in Polish *Maene. lago-wiense* and *Maene. kielcense* (SOBOLEV).

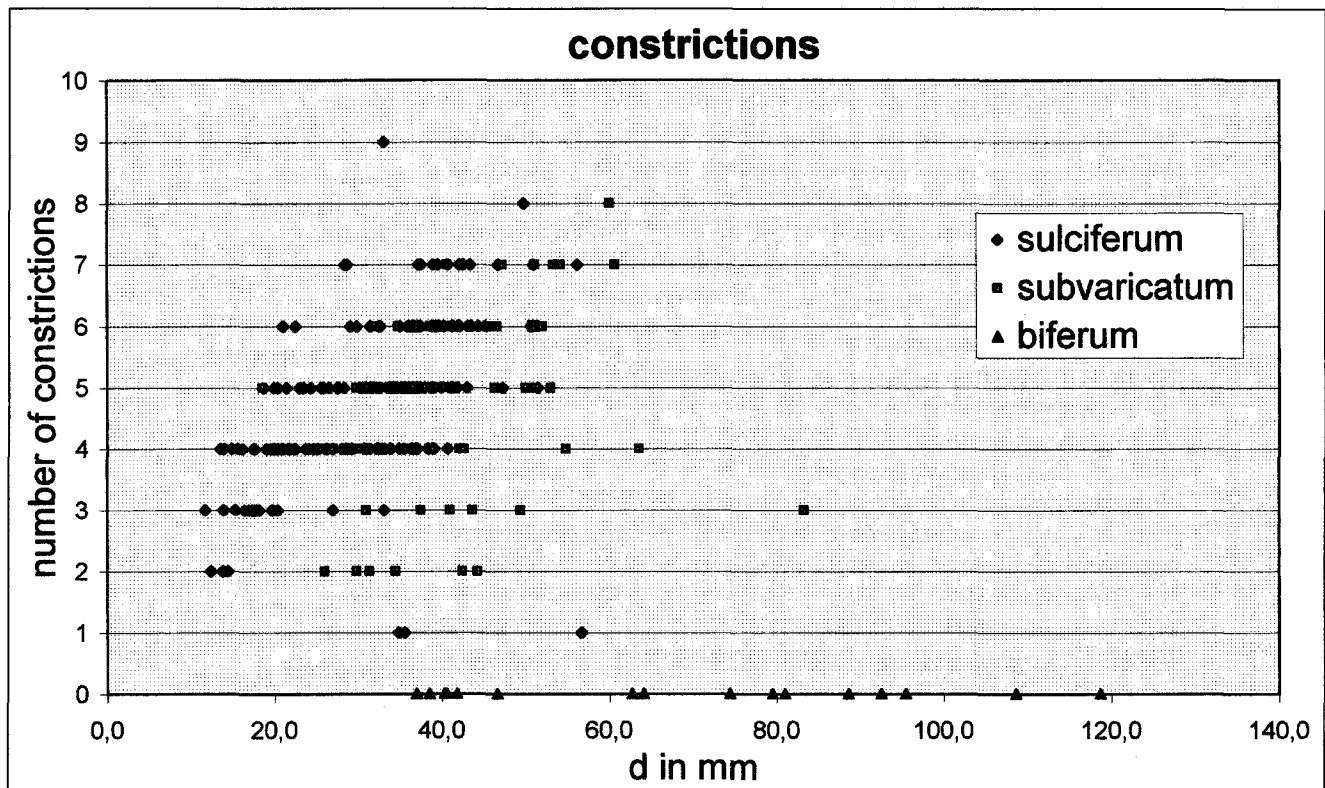
4.3. Mould Constrictions

In many Upper Devonian ammonoids, the presence, absence or course of internal shell thickenings (mould constrictions, varices) is of taxonomic significance and allows the separation of species, or even of genera. In cheiloceratids, for example, subgenera have varices that either follow the aperture and growth lines (*Raymondiceras*), or both features are decoupled (*Cheiloceras*) and the constriction course is highly variable (R.T. BECKER, 1993a). Decoupling has also been observed in oxyconic goniatites such as *Oxytornoceras signatum* BECKER or in parator-



Text-Fig. 11. ▼▼▼
The number of constrictions per whorl in a sequence of four size classes, illustrating first an increase in constriction numbers (A, B), followed by a variable reduction between up to 75 mm diameter (C), and finally a more or less complete reduction in latest ontogeny (D).





Text-Fig. 12.

Numbers of complete and incomplete constrictions against diameter in Hassi Nebech maeneceratids, using the subspecies terminology of J. KULLMANN (1960).

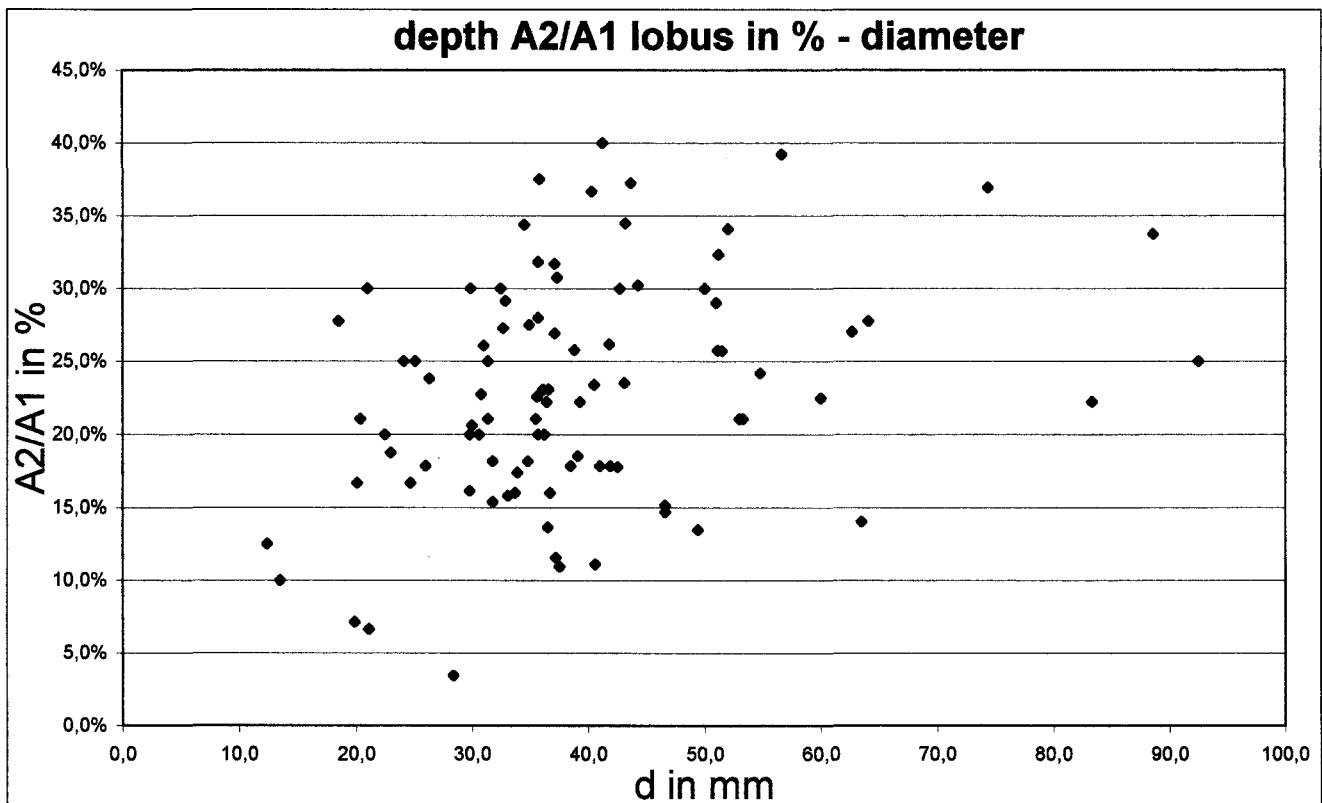
noceratines (V. EBBIGHAUSEN et al., this vol.). In Devonian Prionoceratidae, such as *Prionoceras*, *Mimimitoceras* and *Balvia*, the spacing of true shell constrictions and of associated internal thickenings tends to be very regular whilst there is a great variability in the closely related *Rectimitoceras* (R.T. BECKER, 1996) which has varices but no shell constrictions in mature stages.

In sporadoceratids, strong mould constrictions characterize some species (e.g., "*Sporad.*" *varicatum*) but are lacking in others or are restricted to ventral shell parts. J. KULLMANN (1960) tried to make sense of species names introduced by D. SOBOLEV (1914) and W. LANGE (1929) and distinguished various subspecies of "*Sporad. biferum*" without, with complete, or with only ventral varices. This was followed by B.I. BOGOSLOVSKIY (1971) but R.T. BECKER (1993a) argued that there is only an ontogenetic change between three morphotypes ("*sulcifera*", *subvaricata* and *bifera*", see examples on Pl. 1 and 2). The Hassi Nebech fauna is used to test this assumption with the help of a larger collection.

The histogram of Text-Fig. 10 shows the frequency of constrictions at Hassi Nebech. There is clearly a high variability and near Gaussian distribution with a strong majority of specimens having four to six varices per whorl. Very few specimens (e.g., MB.C.2877 = No. 40, Pl. 1, Figs. 11–12) have eight to nine shell thickenings. Unconstricted specimens (Pl. 2, Figs. 1–2) seem to plot outside the Gaussian curve which would suggest that taxonomic separation of these is justified. The picture becomes clearer if the number of varices is analyzed in four successive size classes ($d < 25$ mm, 25–50 mm, 50–75 mm, > 75 mm; Text-Fig. 11). Small specimens have on average four constrictions per whorl, and the number increases to five in the next class. At the same time, a minority of individuals lacking constrictions appears (see MB.C.2886,

Pl. 1, Figs. 9–10). In the third class, the population has split into a dominant part with increased numbers (frequency maximum at seven/whorl) and a now larger group without or with only one constriction. Finally, constrictions disappear completely in all but one large specimen. During ontogeny, therefore, first the constriction number increases gradually, but then their formation stops rather suddenly. However, the timing of this change in shell wall secretion differs widely between individuals. Text-Fig. 12 gives an even more detailed picture by plotting the number of complete ("*sulciferum*") and incomplete ("*subvaricatum*") varices against size. Almost regardless of the absolute numbers, larger specimens have only incomplete constrictions. The ontogenetic change from complete to incomplete constrictions is well visible in several specimens such as MB.C.2878 (= No. 102, Pl. 1, Figs. 7–8) and MB.C.2887 (Pl. 2, Fig. 9). As a consequence, caution is needed in using mould constrictions as diagnostic feature in *Maeneceratids*.

In the majority of Hassi Nebech specimens, constrictions are slightly convex over the flank and form a very shallow sinus on the venter. In several individuals, however, the course is very irregular, with a concave course on the flanks (e.g., MB.C.2885 = No. 271, Text-Fig. 1), high asymmetric ventral projections (MB.C.2884 = No. 258) or with significant asymmetry on both conch sides (MB.C.2885 = No. 55). Some of these deviations may have been caused by shell injuries but it is clear that the animals were not seriously affected during their lifetime. The decoupling of shell ornament and of varices anyway shows that thickenings must have formed behind the apertural margin. Strongly asymmetric specimens prove that additional secretion of nacre possibly occurred at least 50° backwards from the aperture. This is in accord with the interpretation of varices as protective measure against



Text-Fig. 13.
Plot of the A_2/A_1 lobe depths ratio against diameter, showing independence of both parameters in ontogeny.

shell-breaking predators which allowed the vulnerable soft body to be retracted behind internal shell ridges. In this context, the course of constrictions is of little functional significance and ventral salients would not have limited the funnel movements when the animal stretched out of the conch. Spacing of varices indicates how far the animal could retract which perhaps influenced the shell orientation during life, since the buccal mass and stomach content may have had some relevant weight. Despite a body chamber angle of ca. 360° , the aperture of a retracted individual was oriented upwards. Constrictions and the lack of an ocular sinus at the aperture can be seen as evidence of regular contact with the seafloor and its potential arthropod predators. Protection became unnecessary from 50–70 mm diameter on, perhaps because of the increased shell thickness. Earlier, the protection of umbilical shell regions was reduced which suggests that predatory attacks came from right below the animals and not from the sides or out of the water column. Common *Thalassinoides*-type burrows in the pelagic facies of the Tafelberg provide evidence for the presence of numerous arthropods which did not preserve as body-fossils.

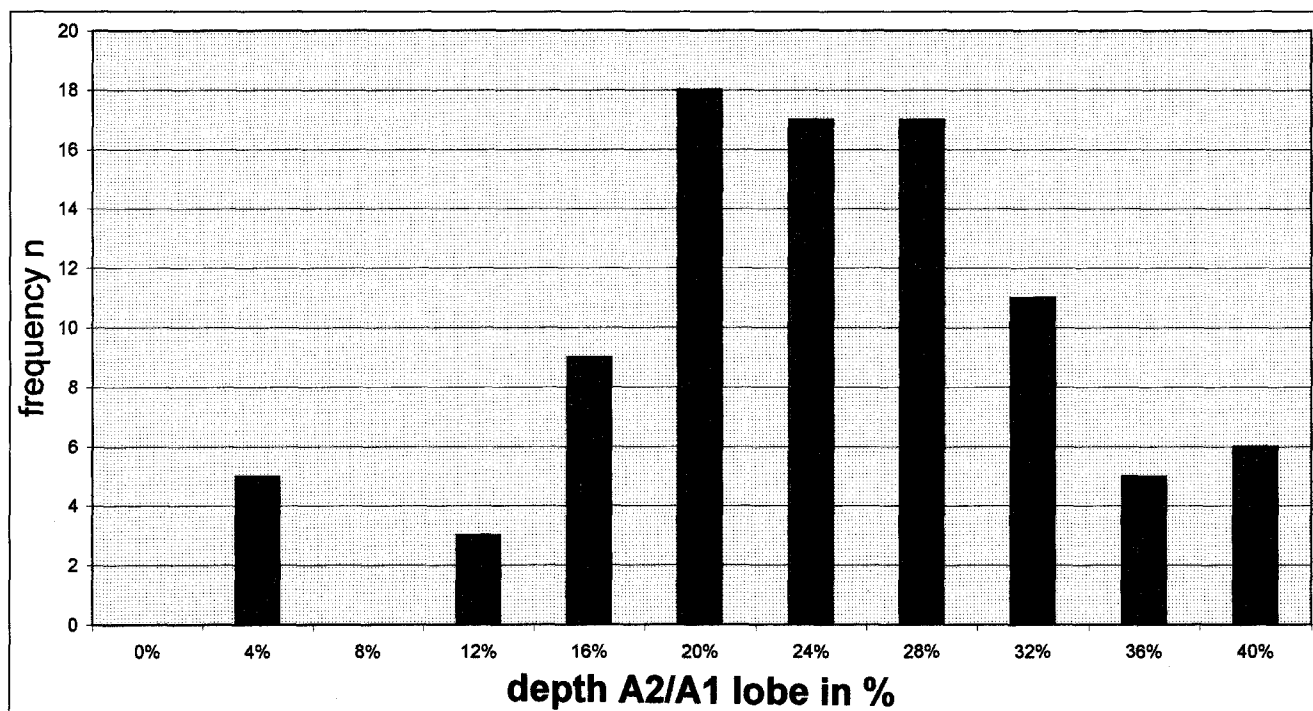
4.4. Sutures

In earlier paragraphs, changes in sutures during maeneceratid phylogeny have been briefly outlined. The Hassi Nebech population was hoped to clarify how far sutural details are more reliable than shell features in recognizing taxa. In Text-Fig. 13 the ratio of A_2/A_1 lobe depths is plotted against diameters. Although an ontogenetic deepening of the A_2 lobe was expected, there is only a very weak trend (regression) to deeper lobes at large size. At the average diameter of the population (around $d = 40$ mm), the depths of A_2 can vary as much as between 10

and 40 % A_1 . However, all morphs seem to be connected by intermediates.

Text-Fig. 14 shows a histogram of A_2/A_1 ratios using 4 % classes. The main fauna has a ratio between 20 and 28 %, as it has often been illustrated for "*Maene. biferum*". The frequency distribution follows almost a Gaussian curve. Separate is the minority of specimens with very shallow A_2 which seems to confirm the distinction of *Maene. biferum nuntio* of R. T. BECKER (1993a), at least at subspecies level. At the other end of variation, a second small maximum is indicated by forms with A_2 deeper than 36 % A_1 (e.g., MB.C.2879 = No. 130, MB.C.2880 = No. 136, Pl. 2, Figs. 5–6). Such forms are intermediate to *Maene. latilobatum* with $A_2 = \text{ca. } 50\% A_1$. In the Canning Basin, similar forms were included by M. S. PETERSEN (1975) in *latilobatum*.

Despite the intergradation between *Maene. subvaricatum* ["*biferum*"] and *latilobatum* in the fauna studied, the separation of both species can probably be kept. The flood of middle and late Famennian sporadoceratids with small A_2 (<25 % A_1) occurred without intermediates to rare last *latilobatum*. This suggests that a strict division was achieved at a later stage and also proves that the deepening of A_2 did not occur in a simple chronomorphocline. The large Hassi Nebech variation can either be explained by too strong condensation of the sampled unit, leading to a sampling admixture of simple and advanced forms, or the population preserved a sympatric speciation in progress, with still incomplete genetical segregation of advanced morphotypes. This could only be clarified by a study of successive large populations, which, unfortunately, are not (yet) available. In the Canning Basin of Australia, interestingly, *Maene. subvaricatum* has been found in the topmost UD II together with the much more advanced *Maene. milleri*, but not together with *Maene. latilobatum*.



Text-Fig. 14.

Histogram of A_2/A_1 lobe depths ratio against diameter, showing a distinction of forms with extremely shallow A_2 (>10 % A_1 : *Maene. subvaricatum nuntio*), shallow A_2 (20–30 % A_1 : *Maene. subvaricatum subvaricatum*) and a gradual transition to forms with moderately deep A_2 (>35 % A_1 : intermediates to *Maene. latilobatum*).

5. Taxonomy of *Maeneceras*

The analyses of the Hassi Nebech population together with literature data are used for a critical review of published *Maeneceras* s. str. species. The following upper Nehebian (UDII-G to II-I) taxa are kept in the genus:

- *β-Oma-dimeroceras (Sporadoceras) subvaricatum* SOBOLÉV (1914): Holy Cross Mountains, $A_2 < 25\%$ A_1 , outer ventral saddle slightly lower than A_1-A_2 saddle, compressed, with complete to incomplete mould constrictions. This is the oldest available name for UD II forms previously identified as *Maene. biferum*. However, D. SOBOLÉV (1914) has used the same species name twice for different sporadoceratids (p. 35: for a *Maeneceras*, and p. 36: for a *Sporadoceras*) and the original of his Pl. VI, Figs. 5a–b is here-with designated as lectotype. The species seems to range rarely into UD III and is here used for forms with $A_2 = 10\text{--}33\%$ A_1 . Rather thick morphotypes (e.g., R.T. BECKER, 1993a: p. 49, 310, Be 580 = MB.C.2889) are included at present but may belong to a new subspecies.
- *β-Oma-dimeroceras (Sporadoceras) curvispina* SOBOLÉV (1914): Holy Cross Mountains, $A_2 < 25\%$ A_1 , outer ventral saddle lower than A_1-A_2 saddle, compressed, with only ventral constrictions; here regarded as morphotype and subjective synonym of *subvaricatum*.
- *Sporadoceras biferum* var. *sulciferum* LANGE (1929): Enkeberg (Rhenish Massif), $A_2 < 25\%$ A_1 , compressed, with complete constrictions; here regarded as a subjective synonym of *subvaricatum*.
- *Cheiloceras daminshanense* LIANG (1980): Inner Mongolia, $A_2 = \text{ca. } 25\%$ A_1 , compressed, mould constrictions terminate near the umbilicus; here regarded as subjective synonym of *subvaricatum*.
- *Sporadoceras inusitata* LIANG (1980): Inner Mongolia, $A_2 = \text{ca. } 30\%$ A_1 , compressed, without constrictions; here regarded as advanced morphotype and synonym of *subvaricatum*.
- *Maeneceras biferum nuntio* BECKER (1993a): southern Morocco, A_2 very shallow (<10 % A_1), compressed to moderately thick, with mould constrictions; here transferred as subspecies to *Maene. subvaricatum*.
- *Maeneceras lagowiense* GÜRICH (1896): Holy Cross Mountains, A_2 around 50 % A_1 but with a distinctively low outer ventral saddle, moderately thick, with complete mould constrictions. *Sporadoceras lagowiense* SOBOLÉV (1914) is not a homonym but a *Sporadoceras* s. str. with deep and narrow A_2 .
- *Sporadoceras daminshanense* LIANG (1980): Inner Mongolia, $A_2 = \text{ca. } 40\text{--}50\%$ A_1 but with a rather low ventral saddle (ca. half as high as the A_2-A_1 saddle), relatively thick; here regarded as a thick morphotype and subjective synonym of *Maene. lagowiense*.
- *β-Oma-dimeroceras (Sporadoceras) kielcense* SOBOLÉV (1914): Holy Cross Mountains, $A_2 = \text{ca. } 50\%$ A_1 but with distinctively low outer ventral saddle, compressed, with ventral mould constrictions. A species which is closely related to *Maene. lagowiense*, or perhaps only a subspecies of the latter.
- *β-Oma-dimeroceras (Sporadoceras) praevaricatum* SOBOLÉV (1914): Holy Cross Mountains, $A_2 = \text{ca. } 40\%$ A_1 but outer ventral saddle rather low, moderately compressed at small size, with complete mould constrictions; here regarded as subjective synonym of *Maene. kielcense*.
- *β-Oma-dimeroceras (Sporadoceras) polonicum* SOBOLÉV (1914): Holy Cross Mountains, $A_2 \text{ ca. } 40\%$ A_1 but outer ventral saddle distinctively low, moderately compressed at small size, with complete mould constrictions; here regarded as subjective synonym of *Maene. kielcense*.
- *Sporadoceras biferum* var. *descendens* SCHMIDT (1922): Dreweier (Rhenish Massif), A_2 between 30 and 40 % A_1 but outer ventral saddle flat, forming a stage, similar as in *Lagowites*; compressed. The type material came from UD III but other authors (e.g., W. LANGE, 1929) have re-

ported the species from UD II. It is possible that this range extension is based on inadequate distinction between *Maene. lagowiense*, *kielcense*, and *descendens*.

- *Sporadoceras latilobatum* SCHINDEWOLF (1923): Gattendorf (Franconia), $A_2 = \text{ca. } 50\% A_1$, compressed, adults without mould constrictions. This species seems to range into UD III and is used here for forms with $A_2 = 35\text{--}60\% A_1$. It includes forms with A_2 between 35 and 50 % A_1 which were previously regarded as advanced morphotype (e.g., R.T. BECKER [1993a]: p. 312, Australian material of M.S. PETERSEN [1975]) or new subspecies (R.T. BECKER & M.R. HOUSE, 1997: Text-Fig. 8) of *biferum*.
- *Paralegoceras? milleri* FLOWER & CASTER (1935): Pennsylvania, $A_2 = \text{ca. } 80\text{--}90\% A_1$, narrow tongue-shaped, compressed, without constrictions.
- *Goniatites acutolateralis* SANDBERGER & SANDBERGER (1850/51): Oberscheld (Rhenish Massif), A_2 as deep as A_1 , widely rounded, A_1 - A_2 saddle angular at maturity, lower than the elevated outer ventral saddle, compressed, without constrictions (at maturity).
- *Sporadoceras Sedgwicki* WEDEKIND (1908): A_2 as deep as A_1 and widely rounded, compressed, without constrictions; regarded by H. SCHMIDT (1922), H. MATERN (1931), and R.T. BECKER (1993a) as a median stage and synonym of *Maene. acutolaterale*.
- *Sporadoceras rinkenbachensis* MATERN (1931: p. 40): a nomen nudum.
- *Sporadoceras xinganense* LI (1996: p. 36, 43): probably a nomen nudum.
- *Goniatites hybridus* MÜNSTER (1832): Hurtigwagen (Franconia), a nomen dubium and "disused taxon" (see R.T. BECKER, 1993a: p. 306–307).
- *Sporadoceras Pompeckji* WEDEKIND (1918): Warstein (Rhenish Massif). R. WEDEKIND (1918) briefly introduced a new species characterized by shallow but extremely wide A_2 . The only available syntype, GPIG 389-179, here designated as lectotype, is a somewhat distorted specimen with the siphuncle situated on the outer flank of one side. In this specimen, the defining feature is pathologically altered but B.I. BOGOSLOVSKIY (1971) has illustrated Russian representatives with sutures resembling those of R. WEDEKIND. Most likely, the majority of *Maene. pompeckji* records (e.g., W. LANGE, 1929) are based on *Maene. subvaricatum* with shallow A_2 and the precise stratigraphical range of *Maene. pompeckji* cannot be given at present. A New York specimen identified by M.R. HOUSE as *Sporad. cf. pompeckji* has a rather deep A_2 , which seems to become tongue-shaped at maturity. The suture relief (saddle height/widths ratio) is rather low, as in supposed *pompeckji*. Until more specimens are found, this form is best assigned to *Maene. cf. latilobatum*.
- *Sporad. primaevum* SCHINDEWOLF does not belong to the Sporadoceratidae but is a species of *Praemerocheras* (R.T. BECKER, 1993a). True *Maeneceras* species of UD III-V are as follows:
 - *Sporadoceras pseudocarinatum* PETTER (1959): Saoura Valley (southern Algeria), A_2 ca. 60 % A_1 , narrow, tongue-shaped, compressed, flanks strongly converging, suboxyconic, without constrictions. This species may have been derived from *Maene. latilobatum*.
 - *Sporadoceras tenuidiscus* SCHINDEWOLF (1923): Gattendorf (Franconia): A_2 ca. 90 % A_1 , widely rounded, strongly compressed with flattened flanks and suboxyconic venter, without constrictions. This species may include the alleged UD V *Maene. acutolaterale* of Drewer (H. SCHMIDT, 1922) and it may have descended from *Maene. pseudocarinatum*.
 - *Sporadoceras rotundum* WEDEKIND (1908): Enkeberg (Rhenish Massif): A_2 ca. 40–45 % A_1 , narrow, tongue-shaped, moderately thick (adult $ww/d > 5.50\%$), without constrictions. This species may be identical with N. Gen. III *spiriferum* and would have priority. Thick forms with shallow A_2 (e.g., R.T. BECKER, 1993a: Be 580 = MB.C.2889) are here regarded as morphotype or subspecies of *Maene. subvaricatum*.

An additional new, rare, still undescribed species has been mentioned by R.T. BECKER et al. (1999) from Southern Morocco. It is characterized by deep A_2 lobes (as in *Maene. milleri*) but with low outer ventral saddle.

Plate 1

Figs. 1–2: *Erfoudites* sp.

MB.C.2888, UD IV-A (*Annulata* Event Bed), Kattensiepen, northeastern Rhenish Slate Mountains.

Fig. 1: Detailed view of flank with delicate spiral ornament; $\times 3$.

Fig. 2: View of complete specimen, showing somewhat undulose, slightly biconvex growth lines; $\times 1$.

Figs. 3–4: *Goniatites biferus* PHILLIPS.

Lectotype, IGS.57301, most likely UD IV/V, Lower Petherwin Beds, South Petherwin, SW England (photo by courtesy of M.R. HOUSE).

Fig. 3: Lateral view; $\times 2$.

Fig. 4: Ventral view; $\times 2$.

Figs. 5–6: *Erfoudites ungeri* (MÜNSTER).

Lectotype, BSHGP VII 890, UD IV/V, Schübelhammer, Franconia (re-illustrated from R.T. BECKER, 1992: Pl. 3, Figs. 1a–b).

Fig. 5: Lateral view, showing slightly biconvex ornament and weak ventral mould constrictions; $\times 1$.

Fig. 6: Ventral view, showing the disappearance of a constriction under the shell; $\times 1$.

Figs. 7–8: *Maeneceras subvaricatum subvaricatum* (SOBOLEV).

MB.C.2878 (No. 102), UD II-G, Hassi Nebech, southern Tafilalet, compressed morphotype.

Fig. 7: Lateral view, showing the ontogenetic change from complete to incomplete (ventral) varices; $\times 1$.

Fig. 8: Adoral view; $\times 1$.

Figs. 9–10: *Maeneceras subvaricatum subvaricatum* (SOBOLEV).

MB.C.2886 (No. 85), UD II-G, Hassi Nebech, southern Tafilalet, moderately thick morphotype.

Fig. 9: Lateral view, showing rather early and sudden disappearance of constrictions; $\times 1$.

Fig. 10: Adoral view, showing the asymmetry of the only constriction over the venter; $\times 1$.

Figs. 11–12: *Maeneceras subvaricatum subvaricatum* (SOBOLEV).

MB.C.2877 (No. 40), UD II-G, Hassi Nebech, southern Tafilalet, compressed morphotype with numerous mould constrictions.

Fig. 11: Lateral view, showing the irregular spacing of slightly convex varices; $\times 1.5$.

Fig. 12: Ventral view, showing the very shallow ventral sinus of varices; $\times 1.5$.

Figs. 13–14: *Maeneceras subvaricatum subvaricatum* (SOBOLEV).

MB.C.2876 (No. 132), UD II-G, Hassi Nebech, southern Tafilalet, relatively thick morphotype with shallow A_2 , resembling ?*Maene. rotundum*.

Fig. 13: Lateral view, showing the disappearance of constrictions and sutures; $\times 1$.

Fig. 14: Adoral view, showing the typical sporadoceratid septal face; $\times 1$.

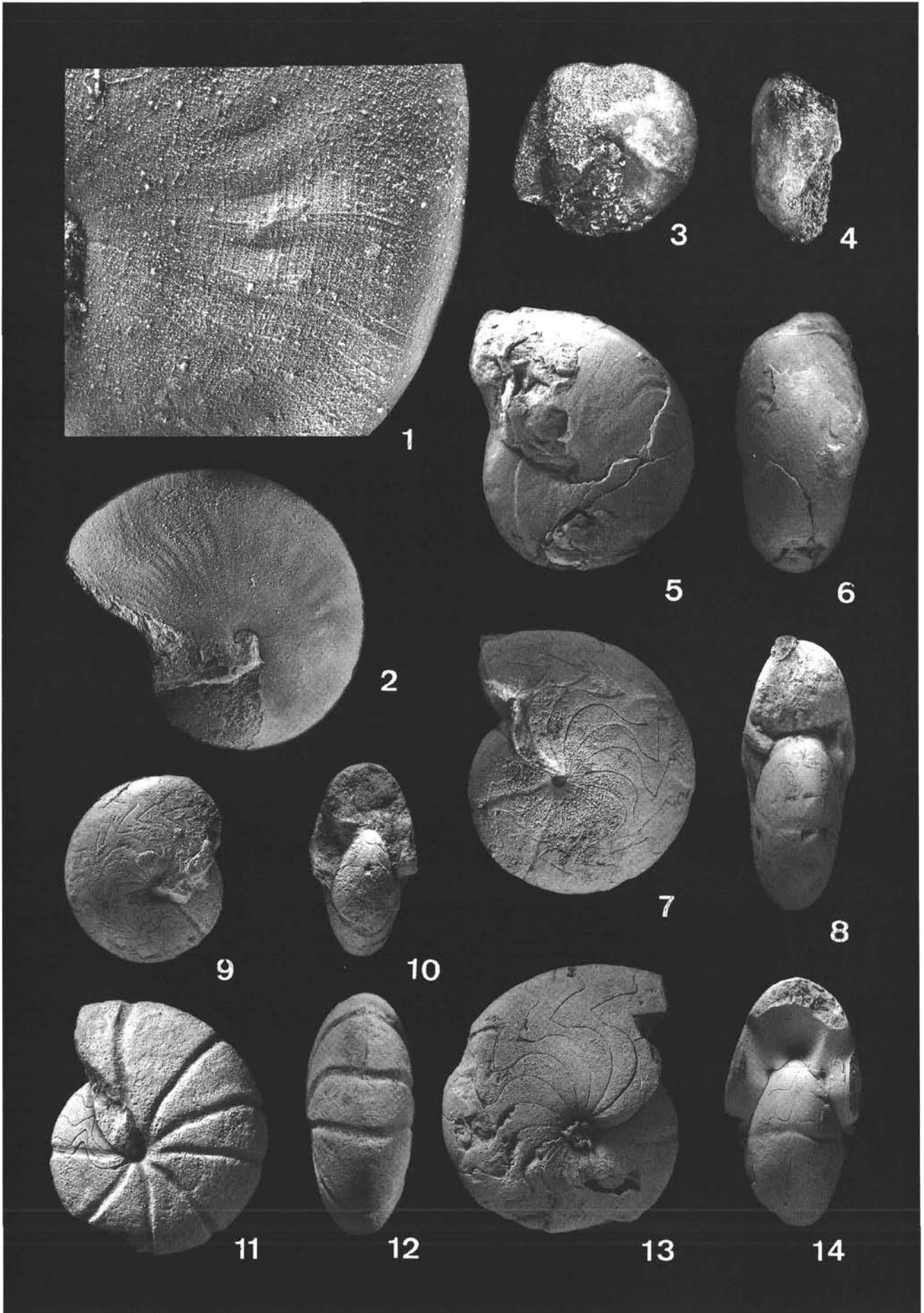
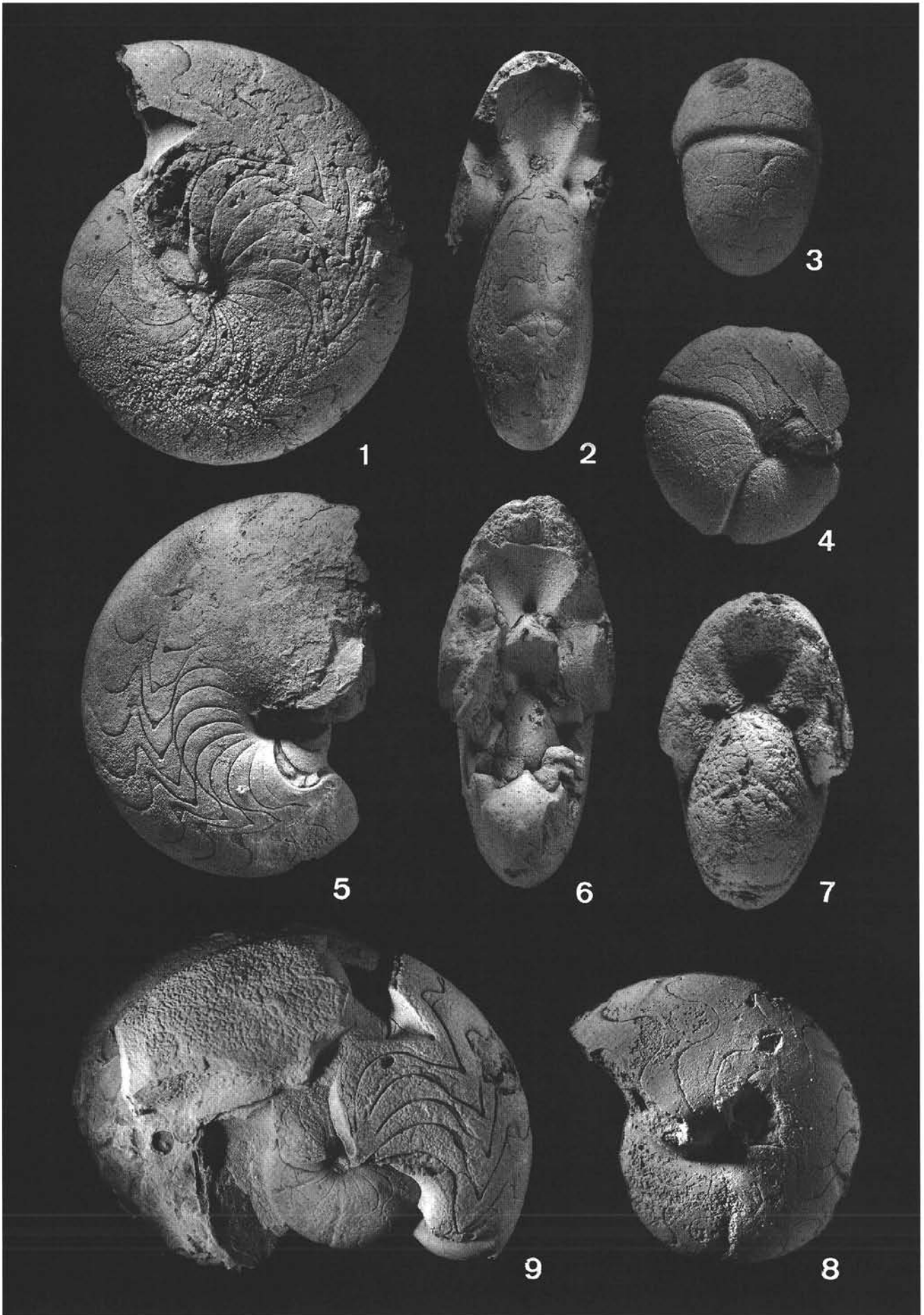


Plate 2

- Figs. 1–2: ***Maeneceras subvaricatum subvaricatum* (SOBOLEV).**
MB.C.2881 (No. 257), UD II-G, Hassi Nebech, southern Tafilalt.
Adult compressed morphotype without constrictions and with shallow A_2 .
Fig. 1: Lateral view, showing typical sutures; $\times 1$.
Fig. 2: Adoral view, showing the septal face; $\times 1$.
- Figs. 3–4: ***Maeneceras subvaricatum nuntio* BECKER.**
MB.C.2875 (No. 240), UD II-G, Hassi Nebech, southern Tafilalt.
Small thick morphotype with complete constrictions.
Fig. 3: Ventral view, showing the very shallow A_2 ; $\times 3$.
Fig. 4: Lateral view; $\times 3$.
- Figs. 5–6: ***Maeneceras latilobatum* (SCHINDEWOLF).**
MB.C.2880 (No. 136), UD II-G, Hassi Nebech, southern Tafilalt.
Adult early morphotype with moderately deep A_2 .
Fig. 5: Lateral view, showing typical sutures; $\times 1$.
Fig. 6: Ventral view, showing septal faces with very deep I-lobe; $\times 1$.
- Figs. 7–8: ***Erfoudites ungeri rotundolobatus* (SCHINDEWOLF).**
MB.C.2881, UD IV/V, loose at Jebel Aguelmous, Maider.
Moderately thick, somewhat intermediate form between *Erf. zizensis* KORN and *Erf. rherisensis* KORN.
Fig. 7: Adoral view, showing ventral mould constrictions, cross-section and septal face; $\times 3$.
Fig. 8: Lateral view, showing the typical, rounded A_1 ; $\times 3$.
- Fig. 9: ***Maeneceras subvaricatum subvaricatum* (SOBOLEV).**
MB.C.2887, UD II-G, Hassi Nebech, southern Tafilalt.
Morphotype with relatively narrow small A_2 , resembling *Erfoudites*, and with mould constrictions which disappear on the last whorl.



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