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Early Ontogeny of three Callovian Ammonite Genera (*Binatisphinctes, Kosmoceras (Spinikosmoceras)* and *Hecticoceras*) from Ryazan (Russia)

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15 Text-Figures, 3 Tables and 8 Plates

Callovian
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Frühstadien von drei callovischen Ammonitengattungen (*Binatisphinctes, Kosmoceras (Spinikosmoceras)* und *Hecticoceras*) aus Rjasan (Russland)

Zusammenfassung

Die embryonalen und jugendlichen Stadien dreier callovischer Ammonitengattungen (*Binatisphinctes mosquensis*, *Kosmoceras* (*Spinikosmoceras*) und *Hecticoceras*) aus Rjasan bei Moskau werden hinsichtlich Gehäusegröße und -geometrie, Schalenstruktur, innerer Merkmale, Mikroornamentation, Wachstumsmodi und Änderungen im Gehäusewachstum untersucht.

Hecticoceras besitzt die kleinsten Ammonitellen, welche bei den anderen beiden Gattungen mit einem Durchmesser von etwa 0,7–0,8 mm größer sind. Trotz unterschiedlicher Größe weisen die Ammonitellen annähernd die gleiche Geometrie auf, nicht jedoch die Juvenilgehäuse mit einer weiteren Windung. Die dorsale und apikale Protoconchwand ist relativ dünn und besteht aus einer einzelnen prismatischen Lage. Dagegen sind die ventrale Protoconchwand und die Wand der ersten Windung dicker. Die lateralen Protoconchwände, die den Umbilikus der Ammonitellen bilden, und die Wand der ersten Windung bestehen aus jeweils zwei prismatischen Lagen. Das erste Perlmutt erscheint in dem ersten Septum nach dem Proseptum und in der primary varix. Die Juvenilschale der ersten postembryonalen Windung besteht aus zwei Lagen, einer äußeren prismatischen und einer inneren perlmuttrigen.

Interne Strukturen wie Flansch, Anheftungsstellen des Prosiphon und des Weichkörpers zeigen qualitative Unterschiede bei den verschiedenen Taxa. Das Mikroornament auf der Außenseite der Embryonalschale wird hinsichtlich Tuberkelgröße und -verteilung im Umbilikalbereich untersucht. Die Mikrotuberkel von *Hecticoceras* sind im Durchschnitt kleiner als die der beiden anderen Gattungen. Auf der Juvenilschale von *Binatisphinctes mosquensis* und *Kosmoceras* (*Spinikosmoceras*) gibt es zusätzlich zur Anwachsstreifung ebenfalls ein tuberkulates Mikroornament. Wachstumsänderungen im Übergang vom Embryonal- zum Postembryonalstadium konnten in allen untersuchten Gattungen nachgewiesen werden, doch nur bei *Binatisphinctes mosquensis* und *Kosmoceras* (*Spinikosmoceras*) kommt es zu einer zweiten Änderung des Gehäusewachstums zwischen der 2. und 3. Windung nach der Ammonitella-Mündung.

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Abstract

The embryonic and juvenile stages of three Callovian ammonite genera, *Binatisphinctes mosquensis* (Perisphinctaceae, Perisphinctidae), *Hecticoceras* (Haplocerataceae, Oppeliidae), and *Kosmoceras* (*Spinikosmoceras*) (Stephanocerataceae, Kosmoceratidae) from Ryazan near Moscow have been examined with respect to size, shell ultrastructure, internal features, micro-ornament, mode of growth, and growth changes.

Hecticoceras has the smallest ammonitella, whereas the latter has a larger diameter of about 0.7–0.8 mm in the other two genera. All ammonitellae show nearly the same geometry in spite of different size, but this does not apply to juvenile stages with one additional whorl. The dorsal and apical protoconch wall is relatively thin and consists of a single prismatic layer whereas the ventral protoconch wall and the wall of the first whorl is somewhat thicker. The lateral walls of the protoconch, which form the umbilical walls of the ammonitella, and the wall of the first whorl comprise two prismatic layers. The first nacre appears in the septum following the proseptum and in the primary varix. The shell of the first postembryonic whorls consists of two layers, an outer prismatic and an inner nacreous.

Internal features like the flange and attachment zones of the prosiphon show qualitative differences in the distinct taxa. The micro-ornament on the embryonic shell surface has been examined with regard to tubercle size and distribution in the umbilical area. On average, the microtubercles on the ammonitella shell surface are smaller in *Hecticoceras* and show a different distribution than in the other two genera. In *Kosmoceras* (*Spinikosmoceras*) and *Binatisphinctes mosquensis*, there is also a tuberculate micro-ornament on the postembryonic juvenile shell in addition to the growth lines. Changes in growth were identified at the transition from embryonic to postembryonic stage in all examined genera, but only *Binatisphinctes mosquensis* and *Kosmoceras* (*Spinikosmoceras*) show a second growth change in the juvenile shell, between the 2nd and 3rd whorl behind the ammonitella edge.

1. Introduction

In the past many scientists have described features from the early whorls of different ammonite genera from the Palaeozoic and the Mesozoic. The first publications have appeared more than a century ago, e.g., BRANCO (1879, 1880), BROWN (1892), and HYATT (1872, 1894). In the beginning of the last century, J.P. SMITH (1901), W.D. SMITH (1905) and GRANDJEAN (1910) described and illustrated different features of the early whorls of ammonoids.

With the development of electron microscopy, the knowledge of composition and structure of early features in the ammonite shell increased rapidly. First, BIRKELUND (1967) and BIRKELUND & HANSEN (1968) described the early shell ultrastructure from Maastrichtian scaphitids and phylloceratids. The publications of ERBEN et al. (1968, 1969), which deals with the early shell ultrastructure of various ammonite genera, is the first which was based on investigations with the scanning electron microscope (SEM). DRUSHITS & KHIAMI (1970), who introduced the name „ammonitella“ for the embryonic shell of ammonoids, described the ammonitella shell ultrastructure of two Lower Cretaceous ammonites.

Further investigations on the structure of the ammonitella shell and of some internal features have been made and published by DRUSHITS et al. (1977a,b), BANDEL (1982), LANDMAN (1982, 1985, 1987, 1994), LANDMAN & BANDEL (1985), TANABE & OHTSUKA (1985), OHTSUKA (1986), BLIND (1988), TANABE et al. (1979, 1980, 1994), WIEDMANN et al. (1996), NEIGE (1997), KLOFAK et al. (1999), and LANDMAN et al. (1999). A comprehensive summary was given by LANDMAN et al. (1996).

In this publication, the early whorls of three middle-upper Callovian ammonite genera, *Kosmoceras* (*Spinikosmoceras*), *Binatisphinctes mosquensis* and *Hecticoceras* from Ryazan (Russia) are described and compared with regard to ammonitella geometry, shell ultrastructure, structure of internal features, size and distribution of the micro-tubercles on the shell surface, and mode of shell growth in the juvenile and adolescent stages.

So far, there has been no study in the Jurassic that aims at the distinction of contemporaneous and associated taxa of different superfamilies, based on populations with preserved early ontogenetic features. It is expected that increased knowledge of embryonic and early juvenile stages will enable a future much better reconstruction of phylogenetic relationships and of palaeoecological specialisations.

2. Material and Methods

2.1. Examined Taxa and Their Source

For the study sufficient material was available for the following three genera:

1) Superfamily: Perisphinctaceae STEINMANN 1890.
Family: Perisphinctidae STEINMANN 1890.
Subfamily: Pseudoperisphinctinae SCHINDEWOLF 1925.
Genus: *Binatisphinctes* BUCKMAN 1921.
Species: *B. mosquensis* (LAHUSEN 1883) (Pl. 1, Fig. 1; Pl. 2, Figs. 1,2).

Subadult specimens of *Binatisphinctes mosquensis* have an evolute conch with a prorsiradiate, primary and secondary dense ribbing which is interrupted on the ventral side by a narrow smooth line. Additionally to the ribbing, parabolic ribs occur on the ventral and ventrolateral side (Pl. 1, Fig. 1C). The number of parabolic ribs on the last whorl varies between 2 and 20 with a frequency of 8–9 at most. The shape of the whorl section is subrectangular in earlier ontogenetic stages and circular in later, subadult stages.

Binatisphinctes mosquensis is described from the *Erymnoceras coronatum* Zone of the upper middle Callovian (MELEDINA, 1988).

2) Superfamily: Stephanocerataceae NEUMAYR 1875.
Family: Kosmoceratidae HAUG 1887.
Genus: *Kosmoceras* WAAGEN 1869.
Subgenus: *Spinikosmoceras* BUCKMAN 1924 (Pl. 1, Fig. 2; Pl. 2, Figs. 3,4).

The heavily ornamented specimens are moderately evolute and show a hexagonal whorl cross section. The ornament comprises ribs and spines. Some of the bigger specimens have been determined as *Kosmoceras* (*Spinikosmoceras*) *pollux* (REINECKE 1818), and as transitional forms to *K.* (*Spinikosmoceras*) *ornatum* (v. SCHLOTHEIM 1820). Most specimens are too small to be determined at species level.

Kosmoceras (*Spinikosmoceras*) *pollux* belongs to middle Callovian strata (GERASIMOV et al., 1996), whereas *K.* (*Spinikosmoceras*) *ornatum* is known from the upper Callovian (MELEDINA, 1988). Available material was not collected in situ, and hence may include specimens from different levels.

The subgenus *Spinikosmoceras* with lappets at the adult aperture was recognized as a microconch (CALLOMON, 1955).

3) Superfamily: Haplocerataceae ZITTEL 1884.
Family: Oppeliidae BONARELLI 1894.
Subfamily: Hecticoceratinae SPATH 1925.
Genus: *Hecticoceras* BONARELLI 1893
(Pl. 1, Fig. 3; Pl. 2, Figs. 5–8).

Hecticoceras possesses platycone conches with a keeled venter. The grade of ornamentation varies interspecifically and intraspecifically, at the same and in different ontogenetic stages. Small specimens are completely smooth-shelled, whereas bigger specimens show a falcate ribbing, lateral nodes and/or ventrolateral ribbing of different intensity. In *H. brightii* (PRATT), a sexual dimorphism has been established (PALFRAMAN, 1969). On the Russian platform, the genus *Hecticoceras* is represented by several species, e.g., *rossiense* (TEISSEYRE), *lunula* (REINECKE), *pseudopunctatum* (LAHUSEN), *nodosulcatum* (LAHUSEN), and *brightii* (PRATT) (GERASIMOV et al., 1996). For this study, mainly small (with preserved ammonitella) and moderately ornamented specimens were selected, resembling *H. brightii*, *H. lunula* and *H. nodosulcatum*. These species are of middle and upper Callovian age (GERASIMOV et al., 1996).

All specimens come from the vicinity of Ryazan (about 200 km southeast of Moscow). Ammonite faunas of this area were described in the 19th century by LAHUSEN (1877, 1883) and TEISSEYRE (1883). Modern publications of Callovian marine faunas from Russia stem from MELEDINA (1988) and GERASIMOV et al. (1996). The material came from commercial fossil traders and was not collected according to stratigraphical principles.

The depicted specimens and the cross and median sections are deposited under MB.C. 3107-3134 in the Museum für Naturkunde, Berlin.

2.2. Preservation

The material comprises phragmocones with 4.3 to 6.5 whorls (including 1.25 whorls of the ammonitella following ERBEN et al. [1968]). The shell diameter extends from 8 to about 30 mm. In most specimens the shell has preserved the original ultrastructure. Only in some specimens of *Kosmoceras* (*Spinikosmoceras*), conellae are identified as prediagenetic alterations.

Generally, the chambers of the phragmocones are completely or partly filled with pyrite. In the latter case there is an empty cavity in the centre of the chamber where idiomorphic pyrite crystals can be observed (Pl. 5, Figs. 6–7). In rare cases, the early chambers are free from matrix, so that septa and organic features like the siphon or the conchiolin layers of the chambers can be observed (Pl. 5, Fig. 1; Pl. 6, Fig. 1).

2.3. Preparation

First, the phragmocones were cleaned ultrasonically for about 30 s. For investigations with SEM, the material was sputter-coated for 300 s. A Ldt S360 Leica Scanning Microscope was used for measurement in the umbilicus of the phragmocones and for photographs of the various ultrastructures.

For further investigations, median and cross sections of the phragmocones have been prepared. For measurements of these, a reflex microscope (Samtron) was used. The obtained data were processed with the programs c3d and Excel.

2.4. Measurements and Terminology

The umbilical width of the ammonitella (uw_A) and the juvenile stage with one additional whorl ($uw_{2.25}$) was measured in the centre of the umbilicus (Text-Fig. 1). The maximum (pd_{max}) and minimum (pd_{min}) diameter of the protoconch, the ammonitella diameter (dm_A), the apertural height of the ammonitella (ah_A), and the ammonitella angle (aa) were measured in median sections of the same specimens (Text-Fig. 2). The ammonitella angle is defined as the angle between the ventral base of the proseptum (ps) and the ammonitella edge (ae) with the centre of the protoconch as rotation centre. The ammonitella diameter is the distance from the ammonitella apertural edge through the protoconch centre to the ventral side of the opposite whorl of the ammonitella (LANDMAN & WAAGE, 1993).

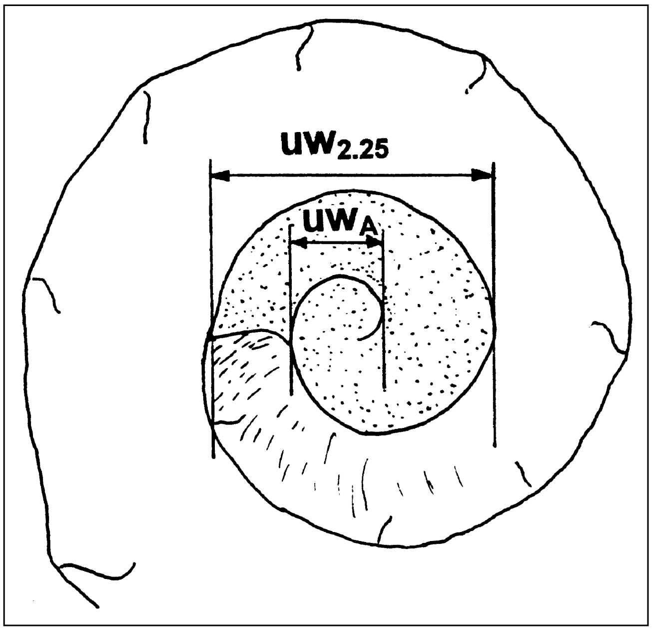
In cross sections, the whorl width (ww_A), the umbilical width (uw_A), the whorl height (wh_A), the apertural height (ah_A), and the conch diameter (dm_A) of ammonitellae were measured (Text-Fig. 2).

The error of grinding amounts to about 5 % in the ammonitella stage, but is smaller in later ontogenetic stages. Therefore, ammonitella shell parameters cannot be elucidated with the same precisions as in juvenile shells and artifically may appear to be more variable.

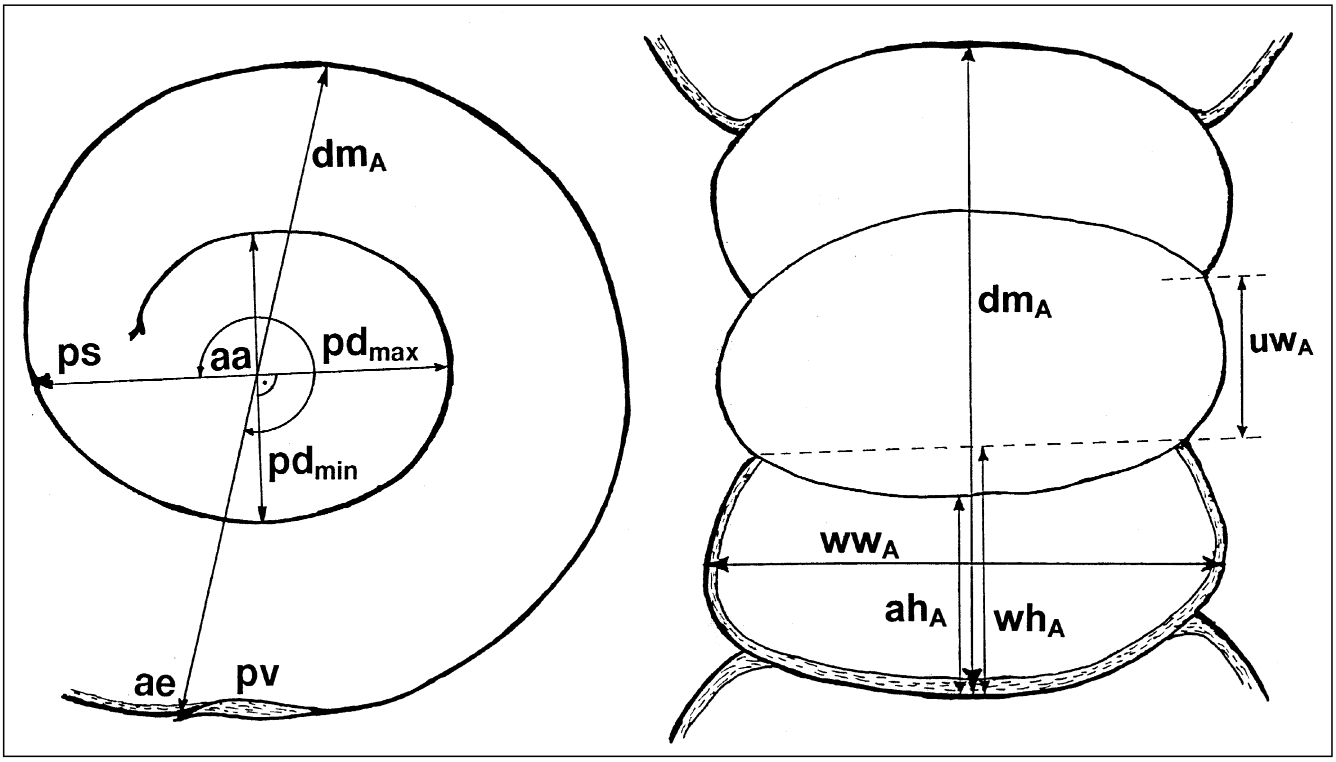
To detect growth changes in ontogeny, the shell diameter (dm), the umbilical width (uw), the whorl width (ww), the whorl height (wh) and the apertural height (ah) were measured for every half whorl in cross sections (Text-Fig. 3). In median sections, the conch diameter and the apertural height were measured for every half whorl, too.

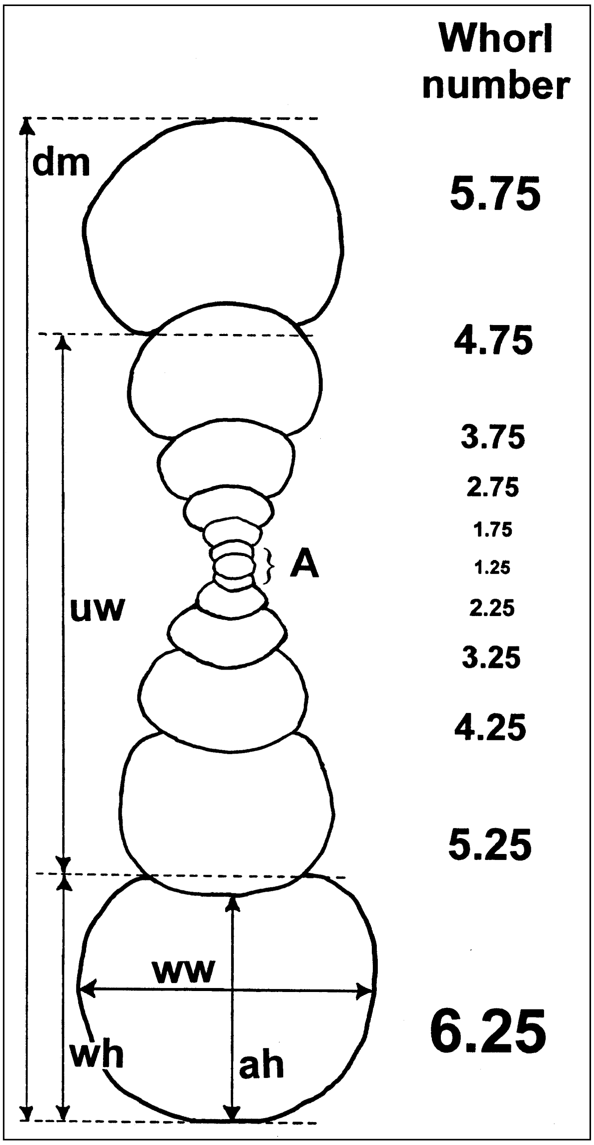
The parameters relative umbilical width (uw/dm) (equivalent to D of RAUP [1966, 1967]), conch width (ww/dm), relative whorl height (wh/dm), and relative apertural height (ah/dm) were calculated for every half whorl.

For the different parts and features of the ammonitella, the terminology of LANDMAN & WAAGE (1982) and LANDMAN & BANDEL (1985) is applied.



Text-Fig. 1.
Definition of the distances measured in the centre of the umbilicus. uw_A = umbilical width of the ammonitella; $uw_{2.25}$ = umbilical width of the juvenile stage with one additional whorl.





Text-Fig. 2. ▲△▲
Schematic drawing of an ammonitella median section (left side) and a cross section (right side) with the measured parameters.
The nacrosepta and the siphon are left out.
aa = ammonitella angle; ae = ammonitella edge; ah_A = apertural heigth of the ammonitella; dm_A = ammonitella diameter; pd_{max} = maximum protoconch diameter; pd_{min} = minimum protoconch diameter; ps = proseptum; pv = primary varix; uw_A = umbilical width of the ammonitella; wh_A = whorl height of the ammonitella; ww_A = whorl width of the ammonitella.

3. Results

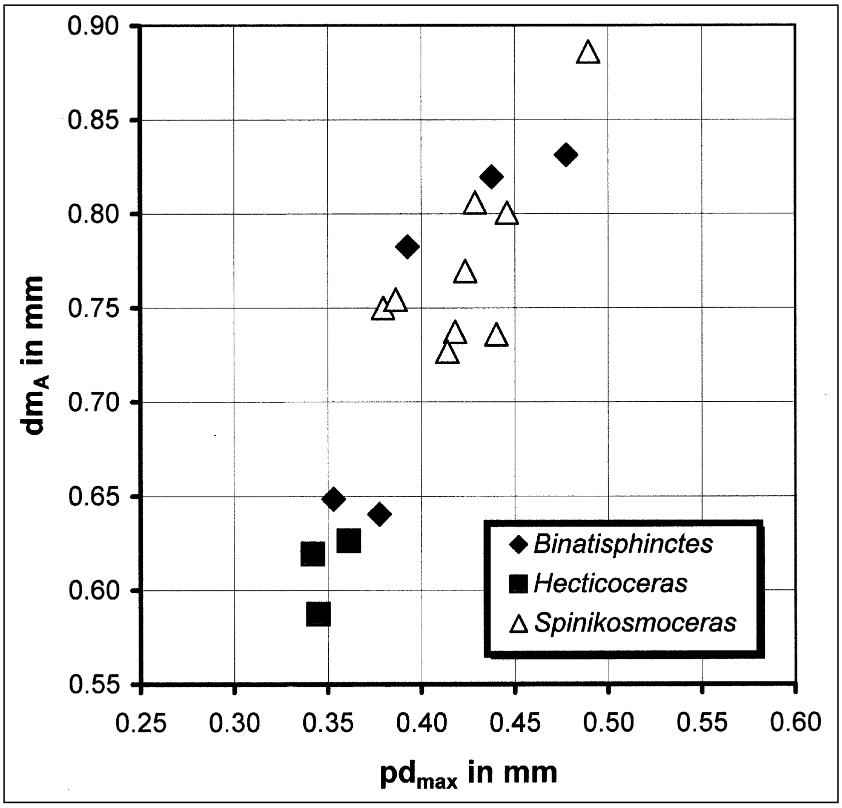
3.1. Geometry and Size of Ammonitellae and of Early Juvenile Stages

There is an obvious size difference between the ammonitellae of *Hecticoceras* and those of the other two examined taxa (Tab. 1). *Hecticoceras* possesses the smallest ammonitellae (mean diameter 0.60 mm; range of 0.55–0.70 mm; 15 values from cross and median sections). Both *Binatisphinctes mosquensis* (mean 0.73; range 0.63–0.83; 20 values) and *Kosmoceras* (*Spinikosmoceras*) (mean 0.77; range 0.65–0.89; 20 values) have bigger embryonic stages. The dm_A values of 0.76 to 0.85 mm in *Kosmoceras* (9 specimens), given by DRUSHITS et al. (1977b), fit the variation determined in this study (Tab. 1).

In PALFRAMAN (1969), a mean value of 0.657 mm and a range of 0.60–0.70 mm is given for the ammonitella diameter of *Hecticoceras brightii*. This nearly corresponds with the values determined here.

In comparison to other Ammonitina and also to all ammonoids, the three genera have relatively small embryonic shells. The ammonitella diameter of other genera of Perisphinctaceae are in contrast to *Binatisphinctes mosquensis* mostly larger than 1.0 mm, and in Haplocerataceae they are clearly smaller than 1.0 mm (LANDMAN et al., 1996: Fig. 6, appendix 1).

Text-Fig. 3. ◀◁◀
Cross section of a *Binatisphinctes mosquensis* conch with the whorl number and measured distances at the last whorl.
The maximum conch diameter at 6.25 whorls amounts to 13.3 mm. Specimen no. MB.C. 3112.
A = ammonitella (whorl number = 1.25); ah = apertural height; dm = conch diameter; uw = umbilical width; wh = whorl height; ww = whorl width.



Text-Fig. 4.
Ammonitella diameter (dm_A) versus maximum protoconch diameter (pd_{max}) in the three examined genera, showing a linear correlation between the two parameters.
The two separated groups concerning *Binatisphinctes* are possibly an artefact of the low number of values. Data stem from measurements of median sections.

In this study, the smallest value of dm_A for *Binatisphinctes mosquensis* is 0.55 mm. This is obviously too small and may have resulted from too strong grinding of this one specimen. The next bigger specimen possesses a dm_A of 0.63 mm.

An intraspecific variation is noticeable. Because of the grinding error of 5 %, the documented variation is possibly larger than the real intraspecific variation within the species. The distance of quartiles (50 % of all values) amounts in *Binatisphinctes mosquensis* and *Kosmoceras* (*Spinikosmoceras*) to about 0.07 mm, in *Hecticoceras* to 0.05 mm.

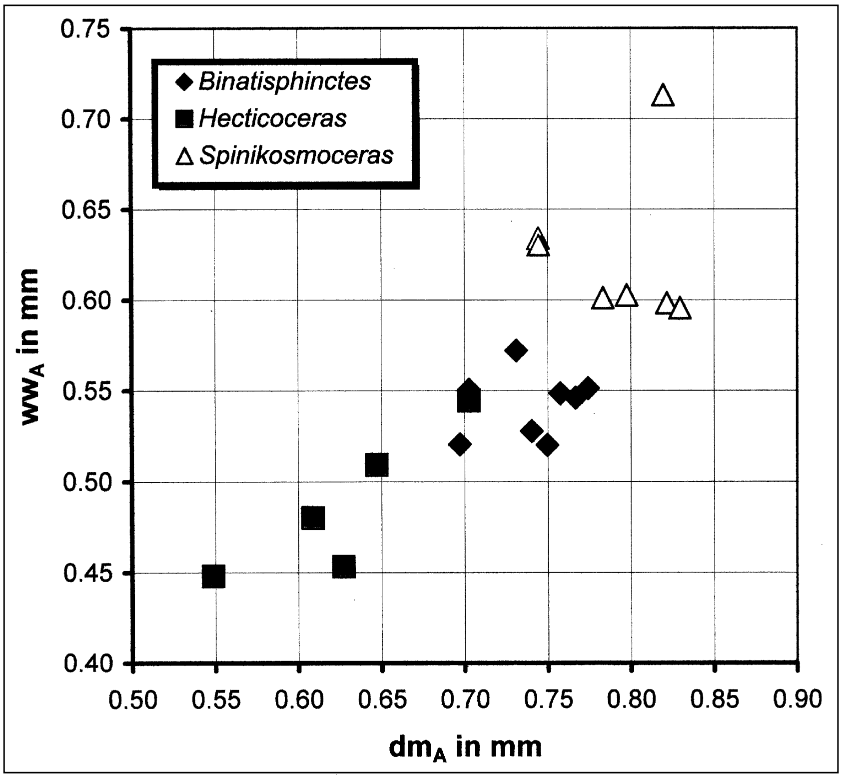
In the examined genera, a positive correlation between the maximum protoconch diameter and the ammonitella diameter is recognizable (correlation value = 0.90) (Text-Fig. 4). This is a common feature, as has been shown by SHIGETA (1993), LANDMAN (1985, 1988), LANDMAN & BANDEL (1985), LANDMAN et al. (1996), NEIGE (1997), TANABE & OHTSUKA (1985), and TANABE et al. (1979, 1994) in many distinct ammonoid genera from different stratigraphic levels. There is also a positive correlation between the ammonitella diameter and the minimum protoconch diameter (correlation value = 0.85) and between maximum protoconch diameter and minimum protoconch diameter (correlation value = 0.89).

The ammonitella angle comprises approximately 280 degrees in all three taxa (Tab. 1). In comparison with other Ammonitina and even with other ammonoids, this is a relatively low value (LANDMAN et al., 1996: Fig. 9, appendix 1).

Ammonitella width and diameter also show a linear correlation (correlation value = 0.82) (Text-Fig. 5). The ww_A/dm_A ratio of *Binatisphinctes mosquensis* ammonitellae is a little bit lower than in *Hecticoceras* and *Kosmoceras* (*Spinikosmoceras*), but possibly this is an artefact caused by the low number of available values (Tab. 3).

The uw/dm ratio of the ammonitellae has a value of about 0.22 in all three genera. In the juvenile stage (whorl number of 2.25) all three genera show a higher uw/dm value than before hatching, but the *Hecticoceras* juveniles are more involute than those of *Binatisphinctes mosquensis* and *Kosmoceras* (*Spinikosmoceras*) (Text-Fig. 6).

The apertural height of ammonitellae was measured on median and cross sections and is correlated with the ammonitella diameter (correlation value = 0.72). In the diagrams of Text-Fig. 7, the relative apertural height (ah/dm) is plotted against the conch diameter of ammonitellae and of juvenile stages with one additional whorl. There is no obvious difference in the relative apertural height of the



Text-Fig. 5.
Ammonitella width (ww_A) versus ammonitella diameter (dm_A), based on measurements of cross sections.
An obvious size difference between the distinct genera is visible.

Table 1.
Values of the ammonitella stage and of the juvenile stage at 2.25 whorls.

	Ammonitella stage (1.25 whorls)			Juvenile stage at 2.25 whorls		
Median and cross sections	*Binatisphinctes mosquensis*	*Kosmoceras (Spinikosmoceras)*	*Hecticoceras*	*Binatisphinctes mosquensis*	*Kosmoceras (Spinikosmoceras)*	*Hecticoceras*
	dm$_{A}$ in mm			**dm**$_{2.25}$ in mm		
mean	0.73	0.77	0.60	1.40	1.53	1.35
median	0.73	0.76	0.61	1.39	1.51	1.32
minimum	0.63	0.65	0.55	1.18	1.40	1.21
maximum	0.83	0.89	0.70	1.58	1.72	1.57
1st quartile	0.70	0.74	0.57	1.34	1.48	1.30
3rd quartile	0.77	0.81	0.63	1.47	1.58	1.40
standard deviation	0.05	0.05	0.04	0.10	0.10	0.09
standard error	0.01	0.01	0.01	0.02	0.03	0.03
number of specimens (n)	20	20	15	21	20	15
	ah$_{A}$ in mm			**ah**$_{2.25}$ in mm		
Mean	0.21	0.24	0.19	0.38	0.42	0.46
Median	0.21	0.24	0.20	0.39	0.42	0.44
Minimum	0.17	0.20	0.13	0.32	0.36	0.39
Maximum	0.26	0.29	0.24	0.48	0.48	0.57
standard deviation	0.03	0.03	0.03	0.04	0.03	0.05
standard error	0.01	0.01	0.01	0.01	0.01	0.01
n	15	15	8	21	20	15
Cross sections, nucleus of conches						
	uw$_{A}$ in mm			**uw**$_{2.25}$ in mm		
mean	0.16	0.17	0.13	0.52	0.52	0.39
median	0.16	0.16	0.13	0.52	0.51	0.39
minimum	0.13	0.13	0.11	0.44	0.44	0.36
maximum	0.21	0.23	0.18	0.59	0.59	0.44
standard deviation	0.02	0.03	0.02	0.04	0.04	0.02
standard error	0.00	0.01	0.00	0.01	0.01	0.01
n	20	15	15	20	16	15
Ammonitella stage (1.25 whorls)						
	Binatisphinctes mosquensis	*Kosmoceras (Spinikosmoceras)*	*Hecticoceras*	*Binatisphinctes mosquensis*	*Kosmoceras (Spinikosmoceras)*	*Hecticoceras*
Median sections	**pd**$_{max}$ in mm			**pd**$_{min}$ in mm		
mean	0.41	0.43	0.35	0.30	0.33	0.26
median	0.39	0.42	0.34	0.26	0.31	0.26
minimum	0.35	0.38	0.34	0.25	0.30	0.24
maximum	0.48	0.49	0.36	0.38	0.37	0.28
n	5	9	3	5	9	3
	Median sections			**Cross sections**		
	aa in °			**ww**$_{A}$ in mm		
mean	283	281	285	0.54	0.62	0.49
median	278	276	285	0.55	0.60	0.48
minimum	274	271	277	0.52	0.60	0.45
maximum	308	298	294	0.57	0.71	0.54
n	5	7	3	8	6	5

Table 2.
Values of the tubercle size.

Tubercle size in µm	*Binatisphinctes mosquensis*	*Kosmoceras (Spinikosmoceras)*	*Hecticoceras*
Mean	3.30	3.06	2.32
Median	3.30	3.02	2.37
Minimum	0.51	0.82	0.47
Maximum	9.93	8.24	4.46
1st quartile	2.56	2.38	1.94
3rd quartile	4.02	3.63	2.76
Standard deviation	1.09	1.00	0.68
Standard error	0.03	0.04	0.03
Number of values	1569	603	758
Number of specimens	22	12	17

ammonitellae of the distinct genera. In contrast to this, the ah/dm ratio of the *Hecticoceras* juveniles with one additional whorl is clearly higher than in the other two genera. This fact implies that selection pressure led to shell differentiation immediately after hatching.

The conformity of the ammonitella angle and the nearly stable proportions of protoconch and ammonitella diameter, conch shape, relative umbilical width, and relative apertural height indicate a nearly identical geometry of the ammonitellae in spite of distinct size in the examined taxa. In the juvenile stage with one additional whorl (whorl number of 2.25), the conches of *Hecticoceras* already show a different geometry than in the other two taxa. They are clearly more involute and possess a higher ah/dm ratio (Text-Figs. 6, 7). In all taxa the uw/dm ratio increases with the transition from embryonic to juvenile stage.

3.2. Shell Structure of the Ammonitellae and of Juvenile Stages

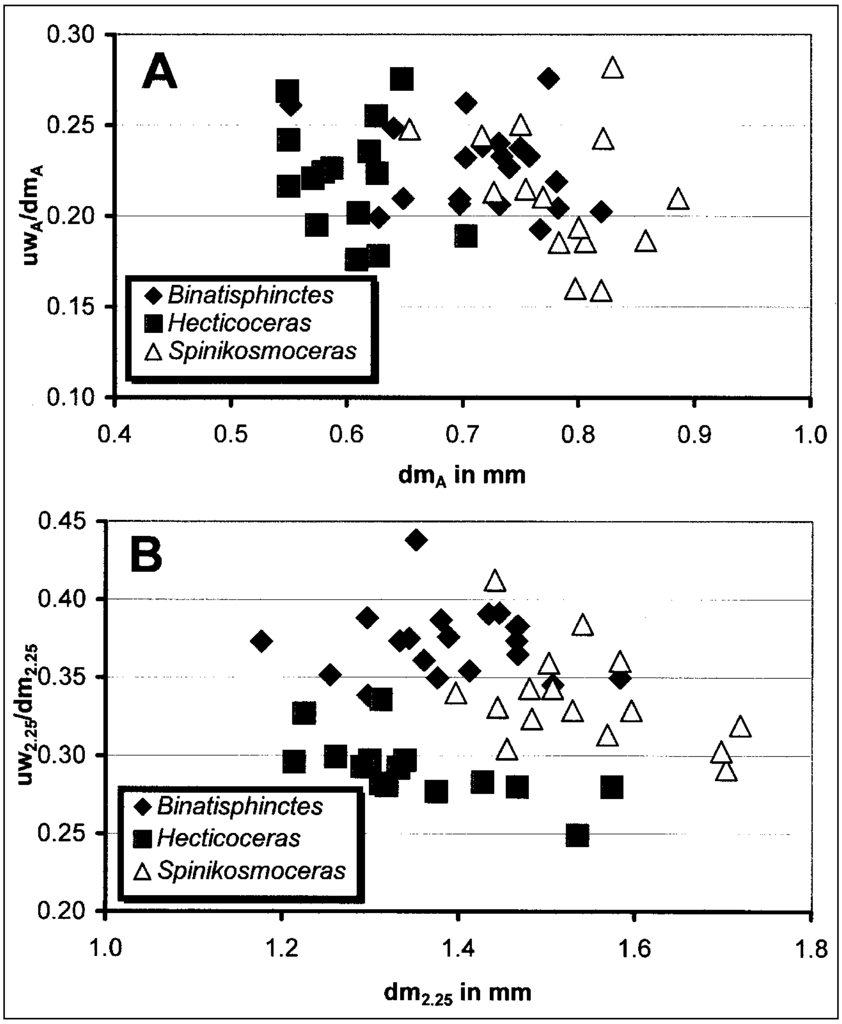
The ultrastructure of embryonic shells was first examined with transmission electron microscope (TEM) by BIRKELUND (1967) and BIRKELUND & HANSEN (1968) in *Saghalinites, Scaphites (Discoscaphites)*, and in *Hypophylloceras*, and with SEM by ERBEN et al. (1968, 1969) in 36 distinct ammonite genera (from the Carboniferous, Triassic, Jurassic, and Cretaceous), and by DRUSHITS & KHIAMI (1970) in the Early Cretaceous *Salfeldiella* and *Zurcherella*. Further investigations were made by KULICKI (1974, 1975, 1979), BIRKELUND & HANSEN (1974), DRUSHITS et al. (1977a, b), TANABE et al. (1980), BANDEL (1982), BLIND (1988), and KULICKI & DOGUZHAEVA (1994). A summary of results can be found in KULICKI (1996).

The embryonic shell ultrastructure of *Kosmoceras* was elucidated by ERBEN et al. (1969), KULICKI (1975, 1979), DRUSHITS & LOMINADZE (1976), DRUSHITS et al. (1977b), and LANDMAN & BANDEL (1985). The other two genera have not yet been examined in this respect.

The protoconch wall structure could be studied in some specimens with partly broken ammonitellae (Pl. 3, Figs. 1–2). In its apical and dorsal parts it consists of only one single layer, probably originally enriched with organic material. The ventral part of the protoconch wall comprises three layers with prismatic ultrastructure (Pl. 3, Figs. 5–6). The inner layer probably corresponds with the proseptum wall which also has a prismatic structure. The two-layered lateral walls of the protoconch are constructed like the wall of the first whorl (Pl. 4, Figs. 1–2).

In *Hecticoceras* and *Binatisphinctes mosquensis*, the first septum following the proseptum possesses a nacreous structure (Pl. 6, Fig. 2). In *Kosmoceras*, this was detected earlier by LANDMAN & BANDEL (1985).

In all three examined genera, the shell of the first whorl up to the beginning of the primary varix is formed identically by two prismatic sublayers (Pl. 3, Figs. 2, 4, 7, 8). The inner one consists of elongated crystals orientated perpendicularly to the shell surface. The outer layer is built



Text-Fig. 6.
A) Relative umbilical width (uw_A/dm_A) versus shell diameter (dm_A) of the ammonitellae.
B) Relative umbilical width ($uw_{2.25}/dm_{2.25}$) versus shell diameter ($dm_{2.25}$) in juvenile stages with one additional whorl. The relative umbilical width of juveniles of all three taxa is higher than in ammonitellae. The *Hecticoceras* juveniles are more involute than the juveniles of the other two genera.

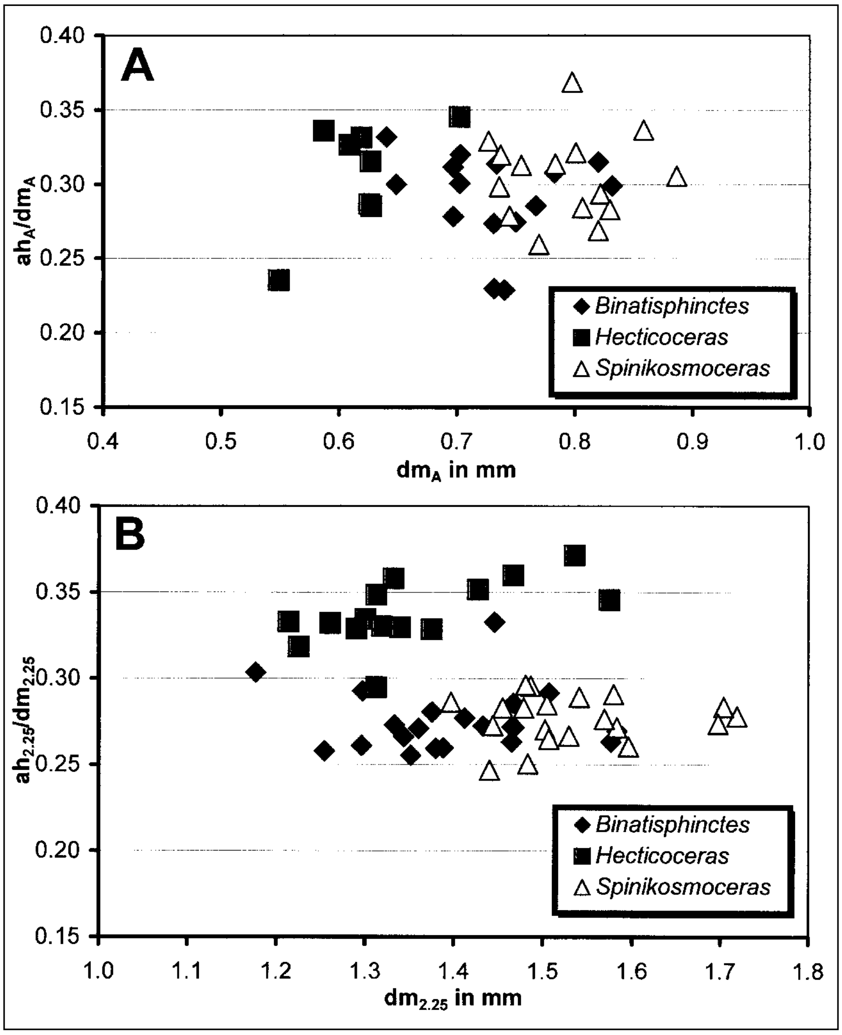
Table 3.
Ontogenic development.
Values from cross and median sections and from the phragmocone umbilicus.
B = *Binatisphinctes mosquensis*; H = *Hecticoceras*; K = *Kosmoceras (Spinikosmoceras)*; min = minimum; max = maximum; n = number of values; wn = whorl number.

		dm			ah/dm			uw/dm			ww/dm			wh/dm		
wn		B	K	H	B	K	H	B	K	H	B	K	H	B	K	H
1.25	mean	0.73	0.77	0.60	0.29	0.30	0.31	0.23	0.21	0.22	0.73	0.78	0.78	0.39	0.42	0.40
	median	0.73	0.76	0.61	0.30	0.31	0.32	0.23	0.21	0.22	0.72	0.76	0.79	0.39	0.41	0.40
	min	0.63	0.65	0.55	0.23	0.24	0.24	0.19	0.16	0.18	0.69	0.72	0.72	0.36	0.38	0.36
	max	0.83	0.89	0.70	0.33	0.38	0.35	0.28	0.28	0.28	0.78	0.87	0.82	0.44	0.48	0.46
	n	20	20	15	15	15	8	20	15	15	8	6	5	8	6	6
1.75	mean	1.01	1.11	0.89	0.29	0.30	0.33	0.34	0.31	0.31	0.67	0.68	0.67	0.37	0.40	0.42
	median	1.02	1.10	0.88	0.28	0.30	0.33	0.34	0.31	0.31	0.67	0.68	0.67	0.37	0.40	0.43
	min	0.82	1.00	0.81	0.25	0.24	0.28	0.31	0.21	0.26	0.65	0.67	0.66	0.35	0.33	0.40
	max	1.16	1.24	1.03	0.36	0.38	0.36	0.38	0.38	0.33	0.69	0.72	0.70	0.38	0.45	0.44
	n	21	20	15	21	20	15	19	16	15	8	6	6	8	6	6
2.25	mean	1.40	1.53	1.35	0.28	0.28	0.34	0.37	0.34	0.29	0.64	0.64	0.58	0.34	0.37	0.42
	median	1.39	1.51	1.32	0.27	0.28	0.33	0.37	0.34	0.29	0.63	0.64	0.58	0.34	0.37	0.42
	min	1.18	1.40	1.21	0.26	0.25	0.29	0.34	0.30	0.25	0.61	0.61	0.55	0.30	0.34	0.38
	max	1.58	1.72	1.57	0.33	0.30	0.37	0.44	0.41	0.34	0.67	0.69	0.62	0.36	0.40	0.46
	n	21	20	15	21	20	15	20	16	15	8	6	5	8	6	6
2.75	mean	1.91	2.07	2.04	0.27	0.26	0.34	0.43	0.39	0.30	0.62	0.62	0.50	0.32	0.33	0.42
	median	1.90	2.08	2.00	0.27	0.26	0.33	0.42	0.39	0.30	0.63	0.62	0.51	0.32	0.34	0.42
	min	1.64	1.84	1.84	0.24	0.22	0.30	0.40	0.35	0.26	0.60	0.57	0.50	0.30	0.31	0.41
	max	2.20	2.33	2.51	0.29	0.30	0.37	0.46	0.44	0.34	0.65	0.69	0.55	0.35	0.35	0.45
	n	21	20	15	21	20	15	7	6	6	7	6	6	7	6	6
3.25	mean	2.61	2.77	3.12	0.27	0.25	0.34	0.44	0.42	0.32	0.61	0.63	0.44	0.32	0.32	0.40
	median	2.57	2.77	3.05	0.27	0.25	0.35	0.45	0.42	0.32	0.62	0.62	0.44	0.32	0.32	0.40
	min	2.22	2.44	2.77	0.24	0.22	0.32	0.40	0.41	0.28	0.57	0.56	0.43	0.29	0.31	0.39
	max	3.05	3.18	3.91	0.28	0.29	0.36	0.47	0.45	0.34	0.64	0.72	0.45	0.34	0.33	0.43
	n	21	20	15	21	20	14	7	6	6	6	6	6	8	6	6
3.75	mean	3.57	3.70	4.71	0.27	0.25	0.34	0.45	0.43	0.34	0.54	0.62	0.38	0.31	0.32	0.40
	median	3.55	3.67	4.57	0.27	0.25	0.34	0.46	0.42	0.34	0.55	0.62	0.38	0.31	0.33	0.39
	min	2.96	3.09	4.10	0.24	0.22	0.32	0.42	0.42	0.31	0.50	0.58	0.36	0.29	0.28	0.38
	max	4.28	4.30	6.08	0.29	0.29	0.37	0.49	0.47	0.36	0.56	0.66	0.41	0.34	0.34	0.42
	n	21	20	15	21	20	15	7	6	6	6	6	6	7	6	6
4.25	mean	4.89	5.03	7.17	0.27	0.26	0.33	0.46	0.43	0.35	0.47	0.58	0.33	0.31	0.33	0.38
	median	4.90	5.02	6.86	0.27	0.26	0.33	0.46	0.43	0.35	0.47	0.57	0.32	0.30	0.32	0.39
	min	3.96	3.96	3.08	0.25	0.22	0.30	0.43	0.39	0.32	0.46	0.54	0.30	0.30	0.29	0.36
	max	6.00	6.12	9.50	0.30	0.31	0.36	0.48	0.48	0.38	0.51	0.65	0.36	0.32	0.37	0.41
	n	20	20	13	20	20	13	7	6	5	7	6	5	8	6	5
4.75	mean	6.66	6.96	10.46	0.27	0.27	0.33	0.48	0.42	0.36	0.40	0.54	0.29	0.29	0.33	0.38
	median	6.75	7.04	9.96	0.27	0.28	0.32	0.49	0.43	0.37	0.41	0.54	0.28	0.29	0.33	0.38
	min	5.34	5.19	7.61	0.25	0.23	0.30	0.45	0.38	0.32	0.38	0.48	0.25	0.28	0.30	0.36
	max	8.35	8.91	15.03	0.28	0.33	0.40	0.49	0.48	0.39	0.43	0.57	0.32	0.31	0.36	0.42
	n	20	20	13	20	20	13	8	6	5	8	6	5	8	6	5
5.25	mean	8.98	9.65	17.58	0.26	0.29	0.34	0.50	0.40	0.30	0.35	0.49	0.23	0.28	0.36	0.44
	median	9.14	9.52	14.95	0.26	0.29	0.33	0.51	0.41	0.30	0.35	0.50	0.23	0.28	0.36	0.44
	min	7.10	6.97	13.94	0.24	0.25	0.32	0.47	0.35		0.33	0.41		0.26	0.32	
	max	11.79	13.63	23.86	0.29	0.35	0.37	0.52	0.45		0.38	0.55		0.30	0.41	
	n	19	16	3	19	16	3	8	6	1	8	6	1	8	6	1
5.75	mean	11.59	10.93		0.25	0.30		0.52	0.41		0.31	0.47		0.27	0.36	
	median	11.47	10.01		0.24	0.29		0.52	0.41		0.31	0.74		0.26	0.36	
	min	9.25	9.87		0.23	0.28		0.49			0.29			0.25		
	max	13.91	12.90		0.28	0.31		0.55			0.34			0.29		
	n	15	3		15	3		7	1		7	1		7	1	
6.25	mean	14.97			0.25			0.53			0.29			0.26		
	median	14.60			0.25			0.53			0.29			0.26		
	min	12.27			0.22			0.50			0.28			0.24		
	max	17.94			0.27			0.56			0.30			0.29		
	n	5			5			4			4			4		

Text-Fig. 7.

A) Relative apertural height (ah_A/dm_A) versus conch diameter (dm_A) of ammonitellae.
All taxa show a relative apertural height of about 0.3.

B) Relative apertural height ($ah_{2.25}/dm_{2.25}$) versus conch diameter ($dm_{2.25}$) of juveniles with one additional whorl. The *Hecticoceras* juveniles show a higher ah/dm ratio than the other genera.



similarly, but the crystals are shorter. The tubercles of the micro-ornament derive from the latter (Pl. 3, Fig. 3; Pl. 7, Fig. 1). Kulicki (1979) described four prismatic layers of the embryonic shell in *Kosmoceras* and *Quenstedtoceras*. The most external is the dorsal wall of the next whorl, the other three belong to the shell of the first whorl. This cannot be confirmed in this study for *Kosmoceras* (*Spinikosmoceras*) and for the other two examined genera. The shell of the first whorl apically of the primary varix clearly shows only a two-layered prismatic structure.

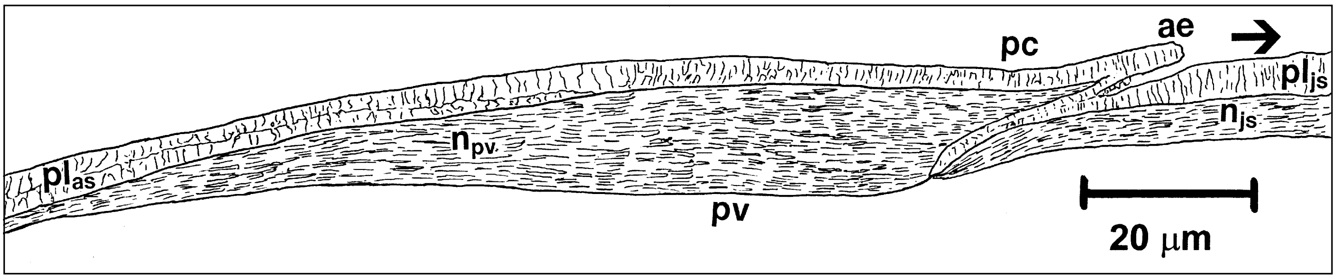
The primary varix near the ammonitella edge, which forms the apertural end of the embryonic conch, consists of an outer prismatic layer and of an inner nacreous swelling. The prismatic layer is formed by two sublayers, the inner one dies out at half way from the beginning of the nacreous layer to the ammonitella edge (Text-Fig. 8; Pl. 4, Fig. 3). At the latter, the prismatic layer, which consists here of only one sublayer, bends with a sharp crease back into the aperture (Pl. 4, Figs. 3–4).

The same feature was depicted by Erben et al. (1969: Pls. 8, 9, 9a) in *Kosmoceras* (*Spinikosmoceras*) and in a few other Jurassic and Cretaceous genera. Remarkable is the fact that an inner prismatic layer (below the nacreous swelling) is present in some, but not in all taxa. In many other ammonite genera, such as *Kosmoceras, Scaphites, Androgynoceras* (Erben et al., 1969: Pls. 8, 9, 9a; Kulicki, 1979: Pl. 45, Fig. 2), *Eupachydiscus* (Tanabe et al., 1980: Text-Fig. 2; Pl. 2, Fig. 3a,b), *Luppovia* (Doguzhaeva & Mikhailova, 1982: Figs. 4, 5), *Aconeceras* (Kulicki & Doguzhaeva, 1994: Fig. 14), it is absent.

In this study, this is also observed in *Binatisphinctes mosquensis* and *Hecticoceras* (Pl. 4, Figs. 3, 4, 6, 7). Other genera already show a fully developed inner prismatic layer at the nepionic swelling (Erben et al., 1969; Kulicki, 1974, 1979; Kulicki & Doguzhaeva, 1994).

The nacreous layer which forms the primary varix is thin in the apical part and consists of only a few rows of lamellae. A single lamella is only 200 to 400 nm thick (Pl. 4, Fig. 5). The number of lamellae which are arranged in rows parallel to the shell surface increases, resulting in a thickening of the nacreous layer and forming the thickest part of the primary varix at a little distance behind the ammonitella edge.

The juvenile shell following the ammonitella edge comprises in *Hecticoceras* and *Binatisphinctes mosquensis* only two layers, an outer prismatic and an inner nacreous layer (Pl. 4, Figs. 6, 7). The same was described by Erben et al. (1969) and Drushits et al. (1977b) in *Kosmoceras*.



Text-Fig. 8.
Drawing of the primary varix of *Hecticoceras* based on SEM photographs.
The line of intersection is parallel to the symmetry plane.
The arrow indicates the direction of aperture (Pl. 4, Fig. 3).
ae = ammonitella edge; n_{js} = nacre of the juvenile shell; n_{pv} = nacre of the primary varix; pc = primary constriction; pl_{js} = prismatic layer of the juvenile shell; pl_{as} = prismatic layer of the ammonitella shell; pv = primary varix.

In *Binatisphinctes mosquensis*, the first parabolic ribs appear on the juvenile shell shortly after the ammonitella edge. In cross section, the outer prismatic layer turns outwards and ends abruptly, whereby a new prismatic layer appears on the inner side of the first. The nacreous layer, however, continues without disruption (Pl. 4, Fig. 7).

In all three examined genera, there are not any differences recognizable in shell ultrastructure of the embryonic shell. Except for the interrupted prismatic layer in *Binatisphinctes mosquensis*, the juvenile shell shows an identical ultrastructure.

3.3. Internal Structures

In some specimens without sediment in the first chambers, some internal features such as the caecum, the flange, and the prosiphon were observable in three dimensions.

The shape of the flange looks different in the examined taxa. In *Hecticoceras*, the flange was broad extending into the protoconch lumen (Pl. 5, Figs. 6, 7) whereas in *Binatisphinctes mosquensis* and *Kosmoceras* (*Spinikosmoceras*), the flange consists only of a small ledge (Pl. 5, Figs. 1, 4; Pl. 6, Figs. 1, 2). The flange in *Binatisphinctes mosquensis* possesses an irregular edge (Pl. 6, Figs. 1, 2). This feature was described by LANDMAN et al. (1999) in *Glaphyrites* (Goniatitina, Upper Carboniferous), in *Scaphites, Hypacanthoplites*, and *Baculites* (Ancyloceratina, Cretaceous).

In one specimen of *Kosmoceras* (*Spinikosmoceras*), a scar from the embryonic soft tissue is conserved at the flange (Pl. 5, Fig. 4), a feature which was observed first by LANDMAN & BANDEL (1985) in a specimen of the same genus and by LANDMAN et al. (1999) in two specimens of the goniatite *Glaphyrites*. The scar is small and long and extends parallel to the whorl axis.

The attachment zone of the prosiphon with the caecum and with the inner side of the protoconch wall is preserved and observable in specimens of *Binatisphinctes mosquensis* and of *Kosmoceras* (*Spinikosmoceras*) (Pl. 5, Figs. 1–3, 5; Pl. 6, Figs. 3–4). In *Binatisphinctes mosquensis*, the attachment of the prosiphon with the protoconch wall is a complex structure, consisting of several parts. Unfortunately it is not completely preserved. However, in *Kosmoceras* (*Spinikosmoceras*) this feature is constructed more simply. The prosiphon is only partly preserved in the attachment zone with the caecum in one specimen of *Kosmoceras* (*Spinikosmoceras*) which has a matrix-free protoconch.

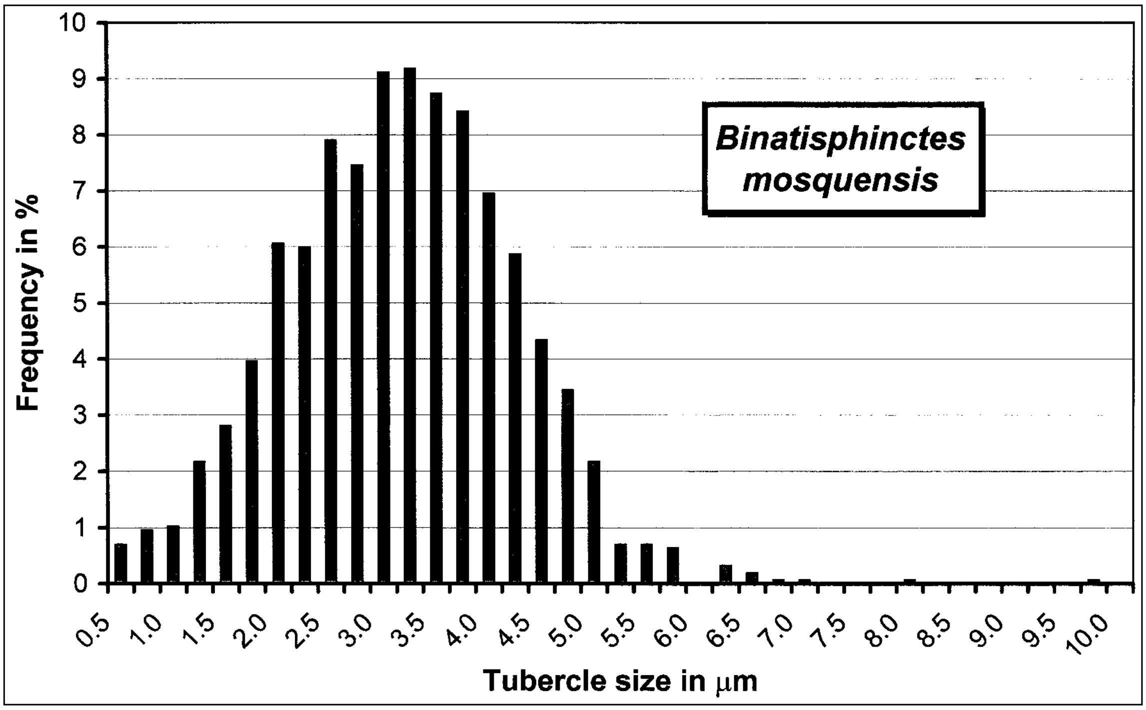
In *Binatisphinctes mosquensis*, the proseptum shows a small amphichoanitic neck. The necks of the first and of the following nacrosepta are prochoanitic (Pl. 6, Fig. 1). Pl. 6, Figs. 5–6 show a structure at the ventral base of the proseptum which resembles the “attachment scar of proseptum”, first described by LANDMAN & BANDEL (1985: Figs. 6, 14, 18) in *Scaphites* and *Baculites*.

3.4. Micro-Ornament

The ammonitellae of Mesozoic Ammonitida are covered with a tuberculate micro-ornament, first described by BROWN (1892) as “pustules” on the embryonic shell of *Baculites*. Later, publications by J.P. SMITH (1901) and W.D. SMITH (1905) were concerned with the tuberculate micro-ornament in both *Scaphites* and *Baculites*. More detailed investigations were exercised with the development of SEM. Some of the most significant publications stem from KULICKI (1975, 1979, 1996), BANDEL (1982), BANDEL et al. (1982), LANDMAN (1985, 1987, 1988, 1994), LANDMAN & WAAGE (1993), LANDMAN et al. (1996, 1998), TANABE (1989), and KULICKI & DOGUZHAEVA (1994).

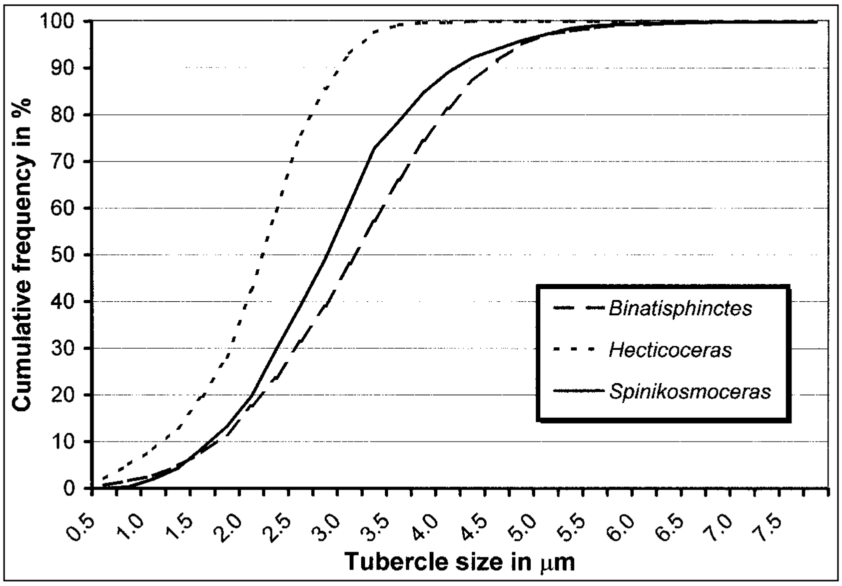
On the outer surface of the ammonitella shell, a tuberculate micro-ornament exists in all taxa examined here (Pl. 7, Figs. 2–8, Pl. 8, Figs. 1–2). The size of the circular tubercles on the flanks was measured under SEM. The frequency of the tubercle size shows a normal distribution; as an example, this is illustrated for *Binatisphinctes mosquensis* (Text-Fig. 9).

Hecticoceras ammonitellae have the smallest tubercles with an average diameter of 2.31 µm (values are given in Tab. 2). In *Kosmoceras* (*Spinikosmoceras*), the tubercles are on average 3.06 µm wide, in *Binatisphinctes mosquensis* 3.30 µm. In Text-Fig. 10 a cumulative frequency diagram shows the tubercle size distribution in all three genera.



Text-Fig. 9.
Frequency histogram of the tubercle size in the umbilical area of *Binatisphinctes mosquensis*.

Text-Fig. 10.
Cumulative frequency diagram of the tubercle size of the examined genera.
Hecticoceras possesses the smallest tubercles, whereas they are in average about 1 µm bigger in the other two genera.



The mean size of the tubercles differs in distinct parts of the ammonitella shell. In *Binatisphinctes mosquensis* and *Kosmoceras* (*Spinikosmoceras*), it decreases in apertural direction, whereas in *Hecticoceras* it is more or less constant.

There are also differences in the distribution of the tubercles on the flanks of the three studied taxa. In *Hecticoceras*, the lateral protoconch walls and the inner flanks of the first whorl are mostly free from tubercles (Pl. 2, Fig. 6; Pl. 8, Fig. 1). In *Binatisphinctes mosquensis*, there is a tendency of a formation of elongated tubercle clusters or sometimes of tubercle rows on the inner flank of the first whorl (Pl. 7, Figs. 3–8). Generally, the tubercles are randomly distributed on the whole outer ammonitella shell, also on parts which were later covered by the next, postembryonic whorl (Pl. 8, Fig. 2). There is no sign of growth lines on the ammonitella shell. The latter appear for the first time on the postembryonic shell immediately in front of the ammonitella edge (Pl. 8, Figs. 5,7).

In well preserved specimens of *Binatisphinctes mosquensis* and *Kosmoceras* (*Spinikosmoceras*), a tuberculate micro-ornament was also found on juvenile shells (Pl. 2, Fig. 4; Pl. 8, Figs. 3–6, 8). Single tubercles have an oval to longitudinal outline. Such juvenile microtubercles are arranged in rows which are running parallel to the growth lines in *Kosmoceras* (*Spinikosmoceras*) and which cross the growth lines in *Binatisphinctes mosquensis*. Microtubercles on the juvenile shell in front of the ammonitella edge first have been depicted by KULICKI (1974) on a specimen of *Quenstedtoceras*, but he regarded them as a kind of growth line ornament. Since tubercles are oblique to growth ornament, at least in some taxa, this interpretation cannot be true (SPREY, 2001)

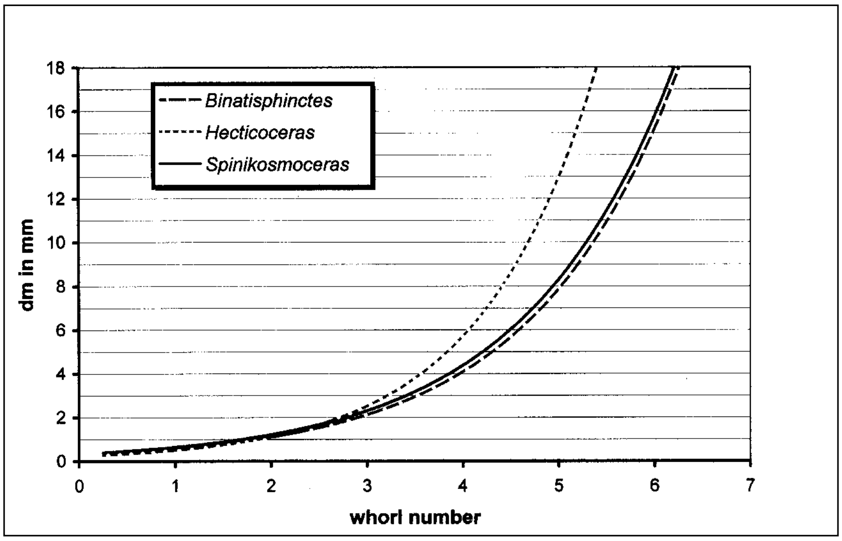
3.5. Growth Changes and Mode of Growth in Ontogeny

The increase of the conch diameter with the whorl number proceeds in an exponential mode. The conch of *Hecticoceras* expands more rapidly than in *Binatisphinctes mosquensis* and in *Kosmoceras* (*Spinikosmoceras*) (Text-Fig. 11). This is also expressed in a higher value of ah/dm in *Hecticoceras* than in the other two genera (Text-Fig. 12). *Kosmoceras* (*Spinikosmoceras*) shows a growth change in ah/dm at a diameter of about 3–4 mm: after a decrease to values below 0.30 at a conch diameter of 3 mm, the ah/dm ratio rate increases again and reaches the same high values as in *Hecticoceras* at a diameter of more than 10 mm. The very high ah/dm values at diameters of about 0.5 mm concern stages with a whorl number of 0.75 (half a whorl before the ammonitella edge) and may have been affected by a high grade of grinding inaccuracy.

The growth of whorl width (ww) changes in ontogeny in all three genera. There is no increase of whorl width in the embryonic stage. In the diagram of Text-Fig. 13, the dots concerning the embryonic stage (until a conch diameter of about 0.8 mm) are arranged horizontally indicating a constant whorl width before hatching. In the postembryonic stage, the whorl width increases rapidly which was already shown, e.g., in *Hecticoceras brightii* by PALFRAMAN (1969: Text-Fig. 4), in different Jurassic ammonoids by CURRIE (1942, 1949), in Upper Cretaceous scaphitids by LANDMAN (1987), LANDMAN & WAAGE (1993), and in the Oxfordian *Creniceras renggeri* by NEIGE (1997).

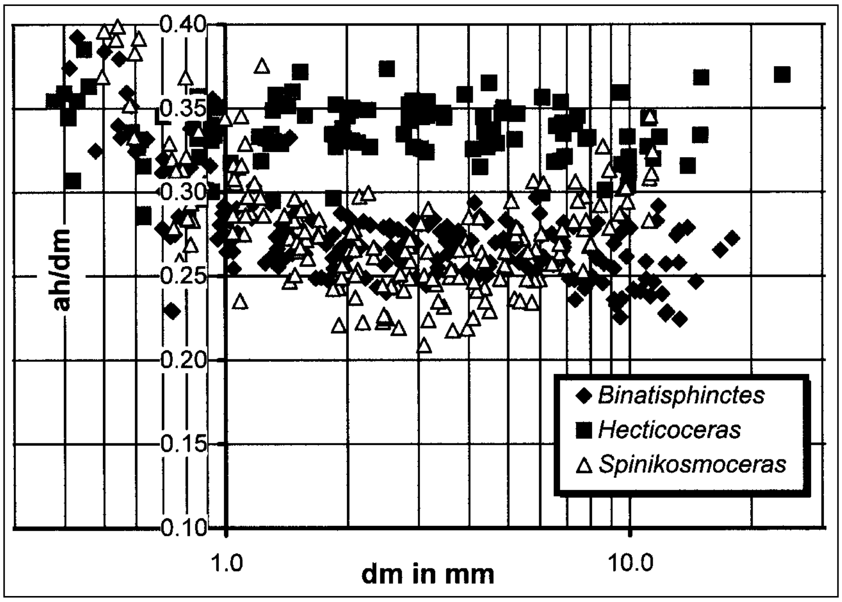
Binatisphinctes mosquensis shows a change of allometric growth at ca. 3 mm resulting in more compressed later stages. In Text-Fig. 13, this is visible at a conch diameter of about 3 mm as a bend in the row of the *Binatisphinctes mosquensis* plot.

The relative umbilical width (uw/dm) increases first in early postembryonic stages of *Binatisphinctes mosquensis* and of *Kosmoceras* (*Spinikosmoceras*), whereas in the more involute *Hecticoceras* it remains more or less constant (Text-Fig. 14). In *Binatisphinctes mosquensis*, the uw/dm ratio catches values



Text-Fig. 11.
Conch diameter (dm) versus whorl number.
From the 3rd whorl on, the *Hecticoceras* conches show a faster increase in dm than the other two genera.

Text-Fig. 12.
Relative apertural height (ah/dm) versus conch diameter (dm) in a logarithmically scaled plot.
In stages larger than 1 mm, *Binatisphinctes* and *Hecticoceras* show a constant ah/dm ratio with growth, whereas in *Kosmoceras* (*Spinikosmoceras*) the ah/dm ratio increases after a minimum at a conch diameter of about 3 mm. *Hecticoceras* possesses relatively higher apertures than the other two genera.



of more than 0.5 at a shell diameter larger than 10 mm. In *Kosmoceras* (*Spinikosmoceras*), the uw/dm ratio first increases after hatching from 0.3 to 0.45 until a conch diameter of about 4 mm, then it decreases to a value of about 0.35 at conch diameters of more than 10 mm. This growth change in *Kosmoceras* (*Spinikosmoceras*) is also visible in the simultaneous change of the relative whorl height. After hatching, the wh/dm ratio decreases from a value of about 0.4 to 0.3, then it increases again to a value of about 0.4 at conch diameters of more than 10 mm.

The growth changes of ww/dm in *Binatisphinctes mosquensis*, and of the uw/dm ratio, the wh/dm ratio and the ah/dm ratio in *Kosmoceras* (*Spinikosmoceras*), occur at a stage of 3–4 whorls (Text-Figs. 11–14).

The mode of growth in the taxa examined mainly is allometric in subadult stages. Only the relative apertural height in *Hecticoceras* and *Binatisphinctes mosquensis* shows an isometric growth (Text-Fig. 12). In *Kosmoceras* (*Spinikosmoceras*), all shell parameters show allometric growth. The values of the relative whorl width, relative umbilical width, and relative whorl height of all three observed genera, and the relative apertural height of *Kosmoceras* (*Spinikosmoceras*) change with shell growth, even if there are no changes of the allometric constants. E.g., the ww/dm ratio of *Hecticoceras* shows a negative allometric growth over the whole ontogeny, whereas in *Kosmoceras* (*Spinikosmoceras*) and *Binatisphinctes mosquensis* only the first postembryonic stage is characterized by an approximately isometric growth, marked by a constant ww/dm ratio between 1 and 3 mm conch diameter (Text-Fig. 15). The umbilical width (uw) in relation to the conch diameter (dm) shows a positive allometric growth in the juvenile stage of *Binatisphinctes mosquensis* and *Kosmoceras* (*Spinikosmoceras*), whereas in *Hecticoceras* it is isometric. In stages larger than 3–4 mm, the growth of the umbilical width still remains positive allometric in *Binatisphinctes mosquensis*, but changes to slightly allometric in *Hecticoceras* and to negative allometric in *Kosmoceras* (*Spinikosmoceras*) (Text-Fig. 14). The mean, median, minimum and maximum values of the conch diameter and the ratios of the other measured distances to the conch diameter are given for every half whorl in Tab. 3.

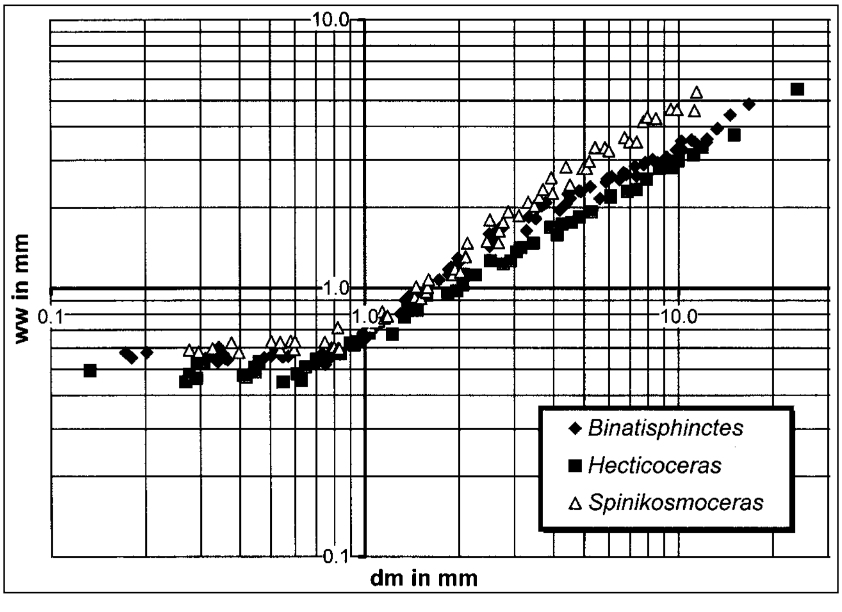
4. Discussion

4.1. Models of Early Ontogeny in Ammonites

The evermore increasing knowledge of embryonic features and of shell structure in Mesozoic ammonoids leads to the development of different models of early ontogeny.

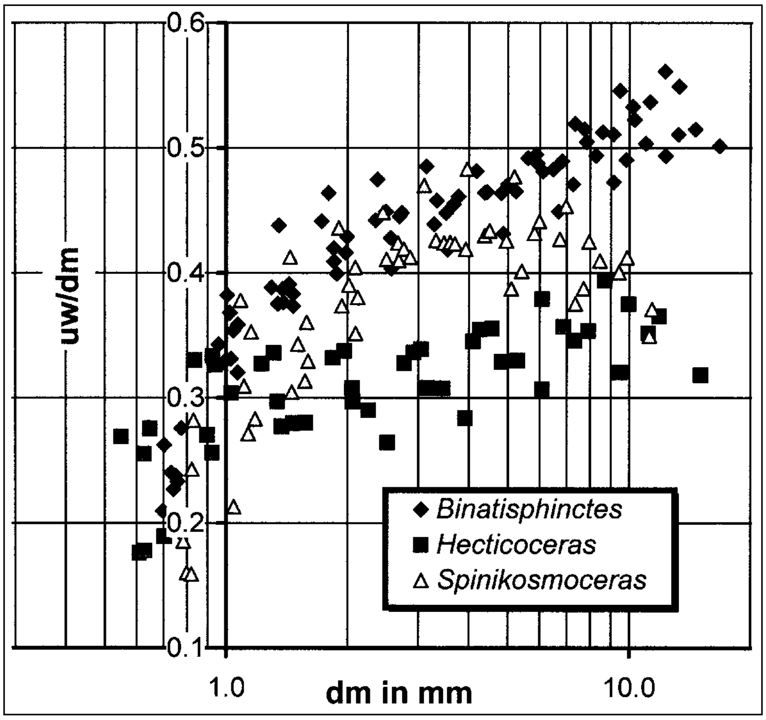
Erben (1962, 1964) and Erben et al. (1968, 1969) proposed three different stages in early ontogeny: an embryonic, a larval, and a postlarval (juvenile) stage. The protoconch was supposed to represent the embryonic stage. secretion of the first whorl was thought by the authors to have happened in a larval stage extending to the formation of the primary varix which was named as “second change in growth”.

Most other authors rejected this hypothesis due to the direct development in all recent cephalopods and proposed only two development stages in the early ontogeny of ammonoids: an embryonic and a postembryonic stage.



Text-Fig. 13.
Log/log scaled plot of whorl width (ww) versus conch diameter (dm).
The first growth change corresponds to the transition of the ammonitella to the juvenile stage. *Binatisphinctes* shows a distinct second growth change at a shell diameter between 2 and 3 mm (at about 3 whorls, see Text-Fig. 11).

Text-Fig. 14.
Relative umbilical width (uw/dm) versus conch diameter (dm) in a logarithmically scaled plot.
Kosmoceras (*Spinikosmoceras*) shows a maximum in shell umbilication at a conch diameter of about 4 mm and a decrease in subsequent ontogeny.
In *Binatisphinctes* the uw/dm ratio increases during the entire ontogeny (as far as observed).
In *Hecticoceras* the uw/dm ratio is nearly constant up to a diameter of about 3 mm, then it slightly increases.



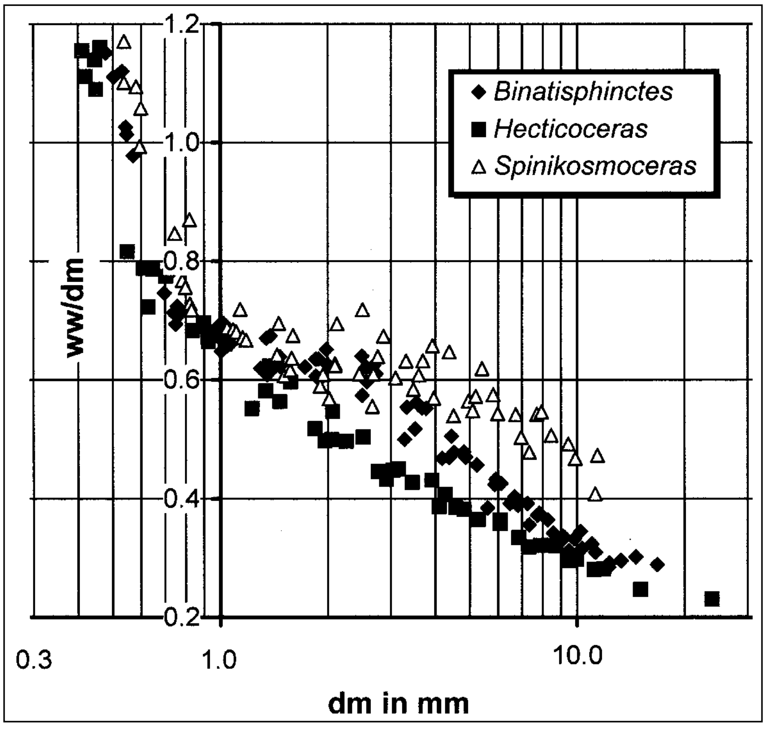
DRUSHITS & KHIAMI (1970) and KULICKI (1974, 1979) proposed an embryonic stage with a continuous secretion of the embryonic shell, similar to the secretion of the postembryonic shell; the hatching is reflected in the ammonitella edge. This was supported by BIRKELUND (1981) and TANABE et al. (1993). The concept of a progressive secretion of an aragonitic primary shell during embryogenesis was developed in opposition to the model with a larval stage of ERBEN et al. (1968, 1969). However, the investigators and supporters of this theory did not consider that the shell growth in the embryonic stage of Mesozoic ammonites may be very different from the progressive accretionary secretion of the postembryonic shell at the apertural margin.

A stepwise formation of the ammonitella shell, described by TANABE et al. (1993), based on findings of Late Palaeozoic ammonites with preserved different growth stages, does not support the concept of DRUSHITS & KHIAMI and KULICKI. It could be as well interpreted as a stepwise calcification of the organic primary shell.

First, BANDEL (1982, 1986) recognized that the lack of growth lines on the ammonitella shell surface indicates a different mode of secretion of embryonic and postembryonic shell. His model of a purely organic primary conch with later calcification derives from observations on the early ontogeny of archaeogastropods. The shell gland secretes the primary conch in organic matter (conchiolin). In a second step before hatching from the egg, the mantle epithelium mineralizes the organic conch.

Further investigations on ammonite embryonic shells from Simbirsk (Russia) in different calcification stages (KULICKI & DOGUZHAEVA 1994), assigned to the Aptian ammonite genera *Aconeceras* and *Deshayesites*, supported the model of BANDEL. The authors distinguished four calcification phases in the early ontogeny. In the first phase, only the outer walls of the ammonitella were mineralized. The second phase is characterized by mineralizing the parts of the protoconch wall which separate the protoconch lumen from the first wall. In the third stage, the proseptum with its ventral basis was calcificied and the nacre of the primary varix was secreted. The fourth phase is characterized by the strengthening of the ammonitella wall through the secretion of additional layers from the inner side of the shell.

In contrast to juvenile stages, ammonitellae of primitive ammonoids from Lower to Middle Devonian show transverse lirae, but no growth lines on their shell surface (KLOFAK et al., 1999). This was interpreted by the authors as evidence for non-accretionary growth. The lirae are ornamental features and their formation possibly was linked with the secretion of the primary organic shell analogous to recent archaeogastropods (BANDEL, 1982). Perhaps they are a sign of stepwise secretion of the primary organic shell. The place free of lirae on the apical part of the protoconch could represent a first cap of the primary shell



Text-Fig. 15.
Conch width (ww/dm) versus conch diameter (dm) in a logarithmically scaled plot.
The decrease of the ww/dm ratio in *Hecticoceras* during ontogeny indicates a negative allometric growth of whorl width in relation to the conch diameter.
Binatisphinctes and *Kosmoceras* (*Spinikosmoceras*) show an approximately isometric growth of whorl width in the juvenile stage between 1 and 3 mm diameter.

and its diameter is possibly adequate to the initial shell gland when secretion begun (KLOFAK et al., 1999). A possibly homologue feature is shown by DOGUZHAEVA (1996) in Permian bactritids.

In 1989, TANABE published a different model in which the ammonitella shell was secreted from an inner and an outer tissue. For a short time, the embryo in the egg had an endocochleate bauplan like in modern coleoids. His model, which is valid only for Mesozoic ammonoids, is theoretically imaginable, but is not based on sufficient evidence in fossil material.

Investigations on the embryogenesis of the extant coleoid *Spirula* and further findings of very well preserved Palaeozoic ammonoids, such as those described by ERBEN (1964), KLOFAK et al. (1999), and LANDMAN et al. (1996, 1999), will hopefully bring more light into the early ontogeny of ammonoids.

4.2. Post-Hatching Mode of Life

There are two preferred theories about the post-hatching mode of life in ammonites. WETZEL (1959) took the view that the young ammonites had a benthic lifestyle. However, many investigators emphasized a planktic mode of life (KULICKI, 1974, 1979; BIRKELUND & HANSEN, 1968; DRUSHITS et al., 1977a; LANDMAN, 1982, 1985; LANDMAN et al., 1996). KULICKI (1974) introduced the term “pseudolarval” for this passive mode of live. The young ammonites fed from the plankton to which they belonged.

Indicators for a planktic mode of life are the fully developed buoyancy apparatus with the protoconch as first gas-filled chamber and with the caecum for liquid absorption and hydrostatic adjustment (HOUSE, 1985). The investigations on 45 ammonoid genera by TANABE & OHTSUKA (1985) show a negative linear correlation between the ammonitella angle and the whorl expansion rate of the ammonitellae. This indicates the necessity of a stable relationship of protoconch volume to the volume of the first whorl up to the ammonitella edge and gives arguments for a planktic mode of life (SHIGETA, 1993).

WESTERMANN (1958, 1996) named the first stage after hatching as “neanic stage”, a term introduced much earlier by HYATT (1894), and distinguished it from the following juvenile stage. The relative high stability of the ammonite conch in the neanic stage (HEWITT, 1988, 1996) indicates an existence in deeper environments. The advantages of this environment were smaller population losses due to decreased predation, but there was a greater probability of killing by rising anoxic waters (WESTERMANN, 1996).

SHIGETA (1993) calculated the buoyancy of Cretaceous ammonitellae and concluded that young ammonites with a completely gas-filled protoconch and a living chamber up to the ammonitella edge are slightly lighter than the surrounding sea water. This did not alter until reaching a stage with a shell diameter of 2.0–2.5 mm. These facts led to the reasoning that in this stage a change in mode of life took place from planktic to nekto-planktic or to nekto-benthic.

The number of septa at the time of hatching of young ammonites is disputed. Some authors, e.g., J.P. SMITH (1901), DRUSHITS & KHIAMI (1970), and SHIGETA (1993), assumed that the just hatched ammonites only had the proseptum, but not yet nacrosepta. WETZEL (1959), KULICKI (1974), and BANDEL (1982), however, reported ammonitellae with more than one septum. BANDEL (1982) noted that it is most probable that Jurassic and Cretaceous ammonites had more than one chamber during hatching. He described ammonitellae of *Baculites* from Jordan with 5–7 septa before the post-embryonic shell was added. In young specimens of the recent coleoids *Sepia* and *Spirula* there are as well more than one chamber while hatching from the egg. LANDMAN (1982, 1985) noted that ammonitellae with more than the proseptum could be fragments of shells of later ontogenetic stages with septa inserted during postembryonic stage. The delicate connection of embryonic and juvenile shell could be a natural weak zone for postmortal breakage.

5. Conclusions

The high grade of conformity in shell ultrastructure of the examined genera from three different superfamilies indicates an identical mode of embryonic development, probably according to the model of BANDEL (1982) because of lack of growth lines on the ammonitella shell.

The nearly stable size proportions of different parts of the embryonic shells suggest the same geometry and necessity for buoyancy and possibly a planktic mode of life immediately after hatching in spite of a different absolute size. With further ontogenetic growth, the shell geometry of the distinct genera developed differently. E.g., *Hecticoceras* conches possess a lower uw/dm ratio and a higher relative apertural height. In most cases, the mode of growth was allometric, e.g., the ww/dm ratio decreases in all three genera during ontogeny with only a short phase of isometric growth in the juvenile stage of *Binatisphinctes mosquensis* and *Kosmoceras* (*Spinikosmoceras*). Growth changes occur at the transition ammonitella – juvenile stage in all three genera and in a stage of 3–4 whorls in *Binatisphinctes mosquensis* and *Kosmoceras* (*Spinikosmoceras*).

The qualitative variation in some embryonic and juvenile features, such as distribution and size of microtubercles, the appearance and form of flange and prosiphon, the mean size of ammonitellae, and the mode of growth and occurrence of growth changes are appropriate characters for taxonomy and for identification of phylogenetic relationships.

Plate 1

Fig. 1: Phragmocone of *Binatisphinctes mosquensis* (LAHUSEN) in lateral (A), apertural (B) and ventral (C) view. Note the parabolic ribs on the venter.
Specimen no. MB.C. 3122/12.

Fig. 2: Heavily ornamented specimen of *Kosmoceras* (*Spinikosmoceras*) sp. in lateral (A) and apertural (B) view.
Specimen no. MB.C. 3129/4.

Fig. 3: Smooth-shelled specimen of *Hecticoceras* sp. in lateral (A) and apertural (B) view.
Specimen no. MB.C. 3134/12.

Scale bar = 10 mm.

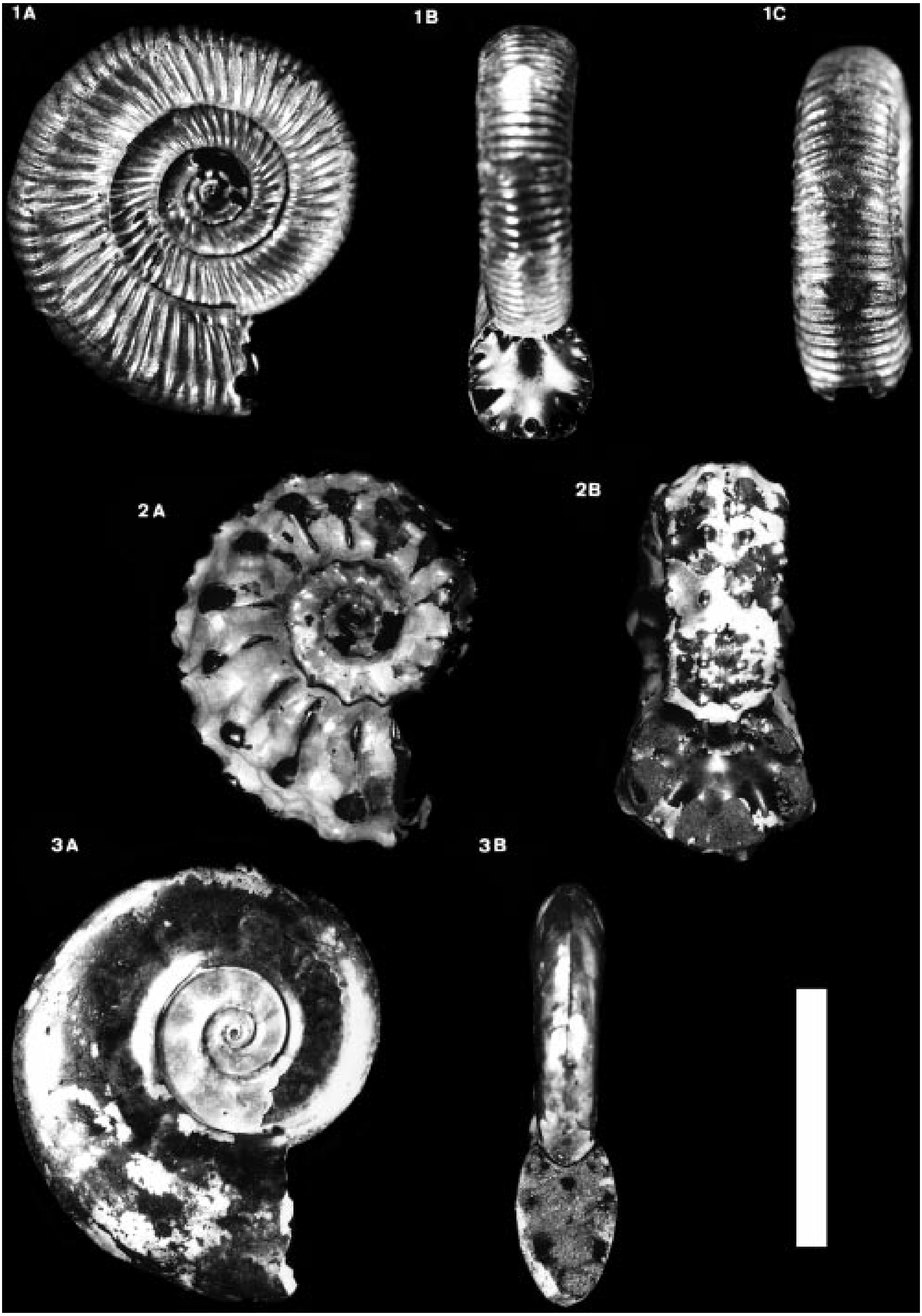

1A
1B
1C
2A
2B
3A
3B

Plate 2

Fig. 1: SEM-photography of a phragmocone of *Binatisphinctes mosquensis*.
In the umbilicus, the ammonitella is visible.
Specimen no. MB.C. 3110.
Scale bar = 2 mm.

Fig. 2: Enlargement of the ammonitella in Fig. 1.
The protoconch lies in the centre of the umbilicus, surrounded by nearly one whorl up to the ammonitella edge. The primary constriction lies a short distance just before the ammonitella edge.
Scale bar = 100 µm.

Fig. 3: Phragmocone of a spiny specimen of *Kosmoceras* (*Spinikosmoceras*) with the ammonitella in the umbilicus.
Specimen no. MB.C. 3127.
Scale bar = 2 mm.

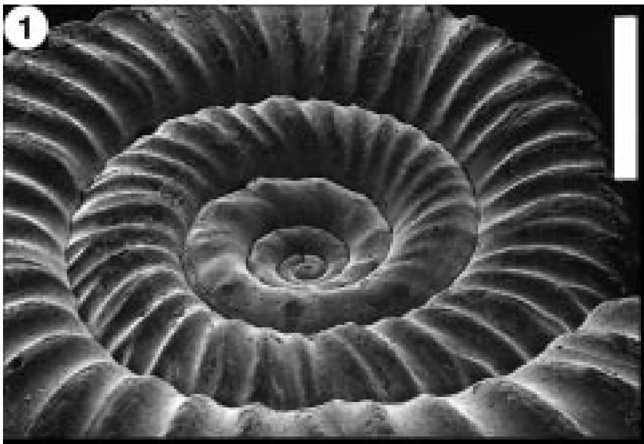
Fig. 4: Ammonitella of *Kosmoceras* (*Spinikosmoceras*) showing the ammonitella edge and the primary constriction.
Same specimen as Fig. 3 with tubercles on the shell surface.
Scale bar = 100 µm.

Fig. 5: A smooth specimen of the genus *Hecticoceras* with preserved ammonitella in the umbilicus.
Specimen no. MB.C. 3131.
Scale bar = 2 mm.

Fig. 6: Ammonitella of *Hecticoceras*. Same specimen as in Fig. 5.
Scale bar = 100 µm.

Fig. 7: Ammonitella and juvenile whorls of *Hecticoceras*.
Same specimen as in Fig. 5.
Scale bar = 200 µm.

Fig. 8: The protoconch as starting-point of the ammonite spiral showing tuberculate micro-ornament.
Same specimen as in Fig. 5.
Scale bar = 50 µm.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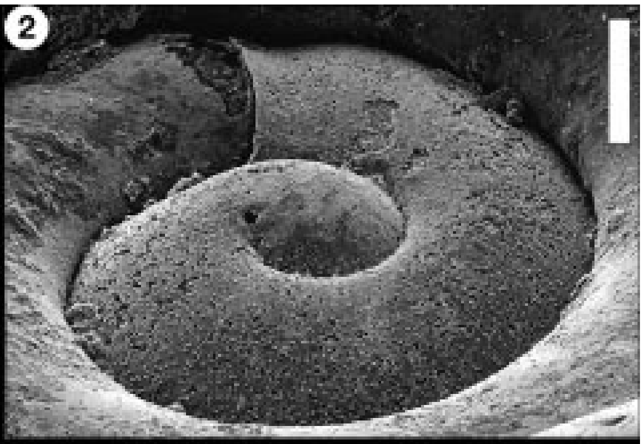
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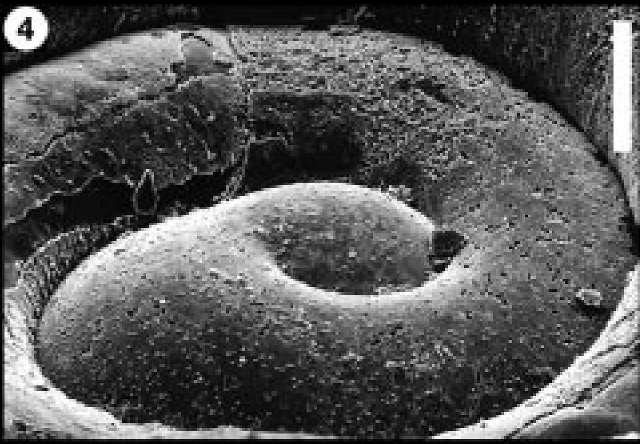
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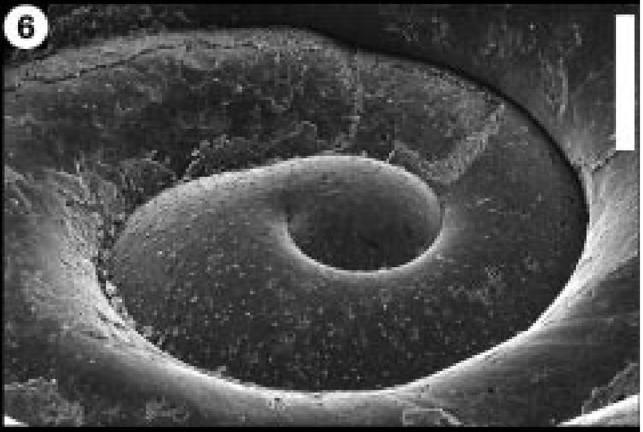
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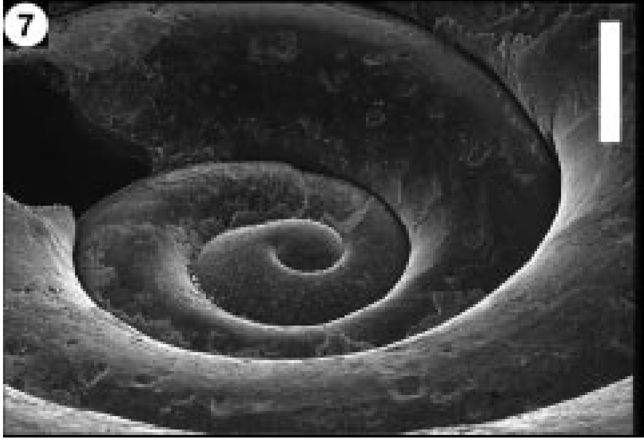
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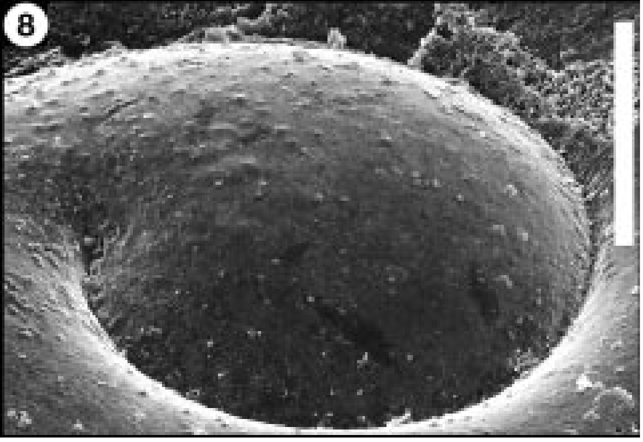
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Plate 3

Fig. 1: The umbilicus of a phragmocone of *Binatisphinctes mosquensis*.
The umbilical area is broken into a section parallel to the median plane.
Specimen no. MB.C. 3109.
Scale bar = 500 µm.

Fig. 2: Part of the ammonitella of *Binatisphinctes mosquensis*.
Same specimen as in Fig. 1. The shell structure in distinct parts of the ammonitella is visible.
Scale bar = 100 µm.

Fig. 3: Shell of the first whorl in a specimen of *Binatisphinctes mosquensis* showing two prismatic layers.
The tubercles derive from the thinner outer layer.
Specimen no. MB.C. 3114.
Scale bar = 10 µm.

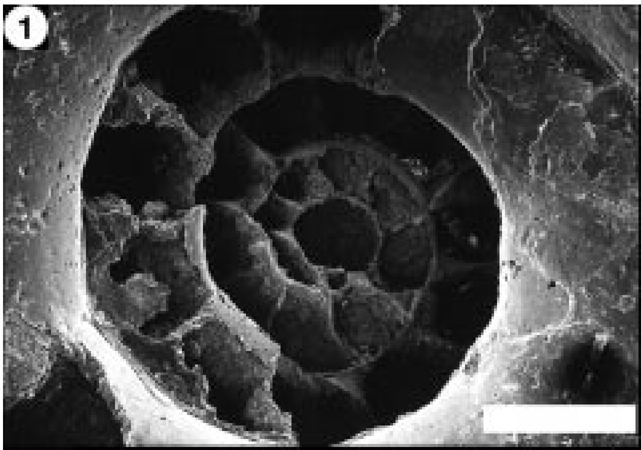
Fig. 4: Shell of the first whorl in *Binatisphinctes mosquensis*.
Enlargement of Fig. 2.
Scale bar = 50 µm.

Fig. 5: Three-layered ventral protoconch wall of *Binatisphinctes mosquensis*.
Same specimen as in Fig. 1. The inner layer possibly continues into the proseptum wall.
Scale bar = 20 µm.

Fig. 6: Enlargement of Fig. 5.
Scale bar = 5 µm.

Fig. 7: Shell of the first whorl of a *Kosmoceras* (*Spinikosmoceras*) ammonitella with tubercles on its surface.
Specimen no. MB.C. 3124.
Scale bar = 50 µm.

Fig. 8: Enlargement of Fig. 7 showing an inner thick and an outer thinner prismatic layer.
Scale bar = 10 µm.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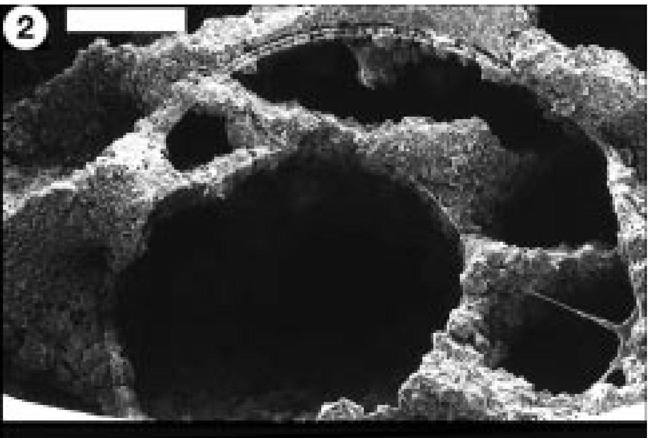
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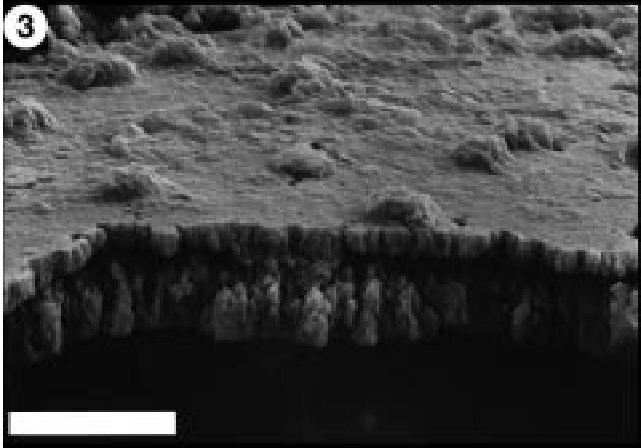
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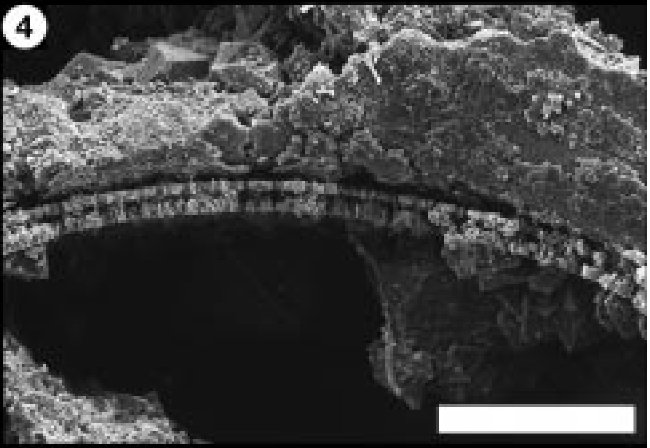
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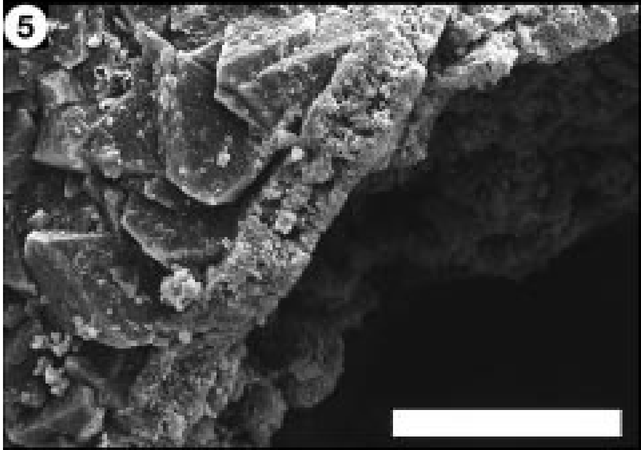
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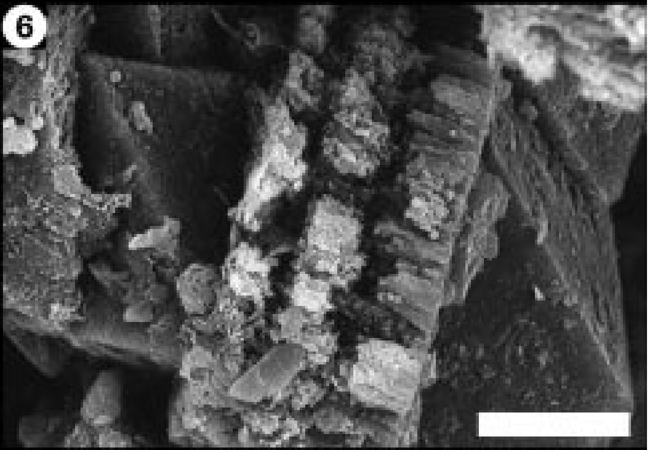
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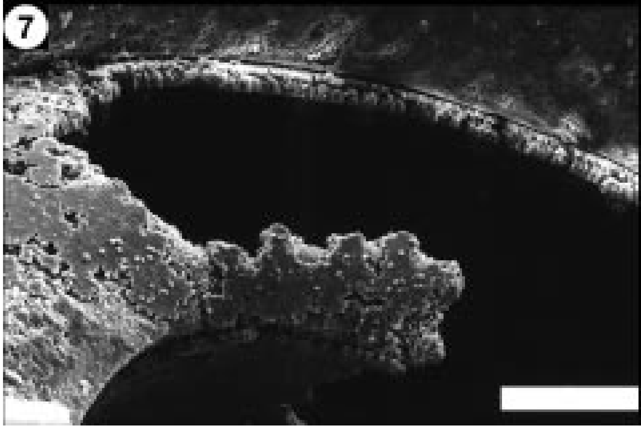
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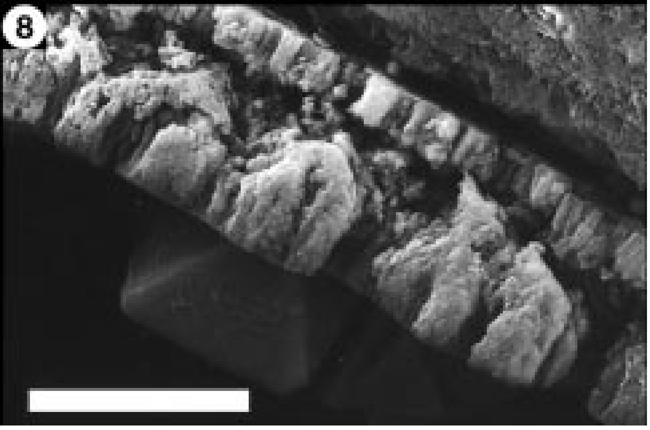
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Plate 4

Fig. 1: Lateral protoconch wall of *Kosmoceras* (*Spinikosmoceras*) with two prismatic layers.
On the left top of the picture the ammonitella edge is visible.
Specimen no. MB.C. 3126.
Scale bar = 20 µm.

Fig. 2: Enlargement of Fig. 1.
Scale bar = 5 µm.

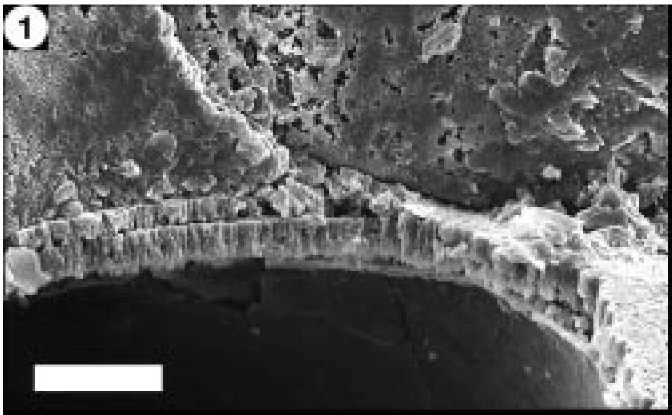
Fig. 3: Section parallel to the median plane of the shell of *Hecticoceras* at the apertural end of the ammonitella with primary constriction, nacreous primary varix and ammonitella edge.
Specimen no. MB.C. 3130.
Scale bar = 50 µm.

Fig. 4: Enlargement of the anterior end of Fig. 3.
In the middle part of the left side of the picture, the nacre of the primary varix is visible, in the lower part there is nacre of the postembryonic shell. On the top of the right side there is the ammonitella edge.
Scale bar = 5 µm.

Fig. 5: Nacre of the primary varix in a specimen of *Binatisphinctes mosquensis*.
Specimen no. MB.C. 3107.
Scale bar = 2 µm.

Fig. 6: Juvenile shell of *Hecticoceras* immediately in front of the ammonitella edge with an outer prismatic and an inner nacreous layer.
Same specimen as in Fig. 4.
Scale bar = 10 µm.

Fig. 7: Shell structure of the juvenile shell in *Binatisphinctes mosquensis*.
Note that the prismatic layer of a parabolic rib bends outwards and is replaced by a new prismatic layer from the inner side. However, the relative thin inner, nacreous layer continues.
Specimen no. MB.C. 3113.
Scale bar = 10 µm.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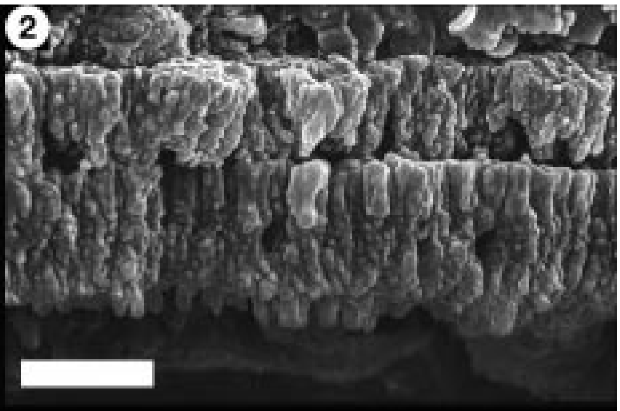
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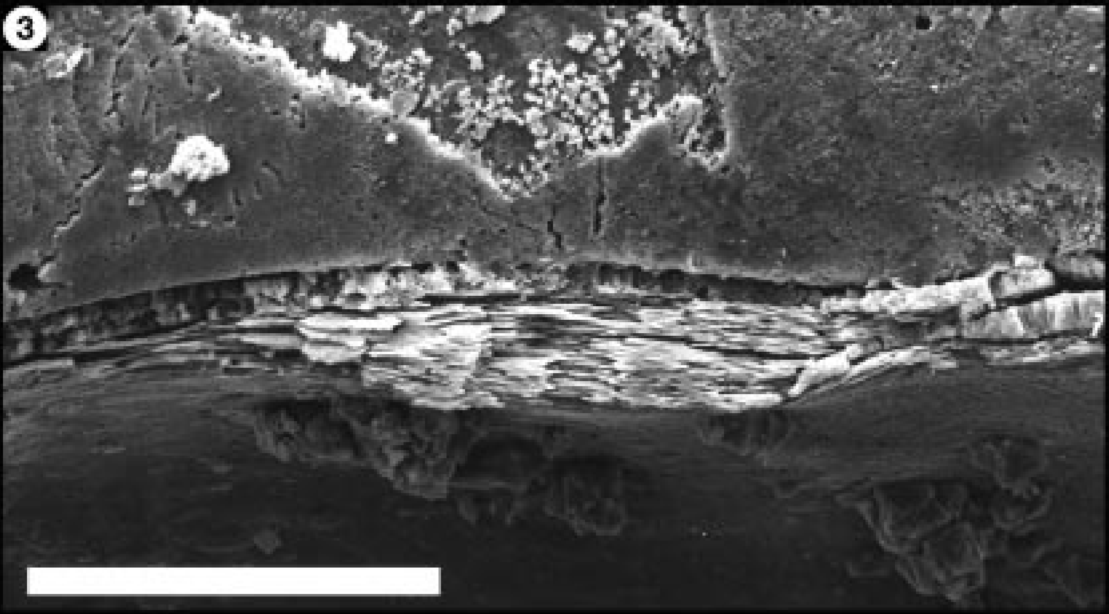
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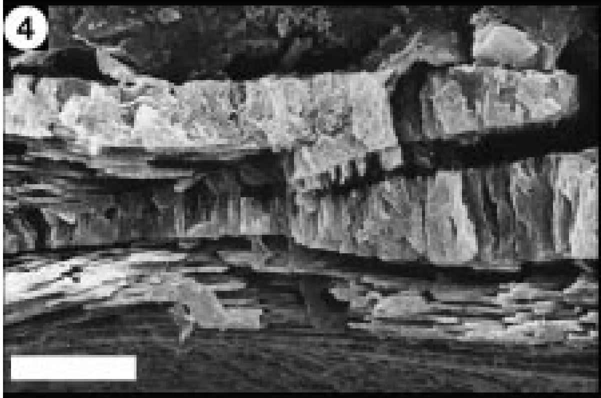
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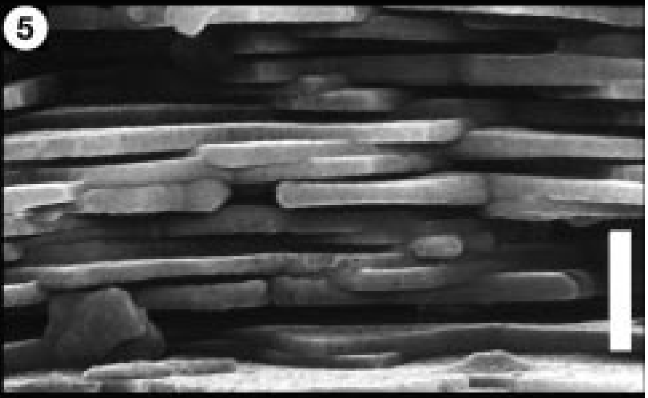
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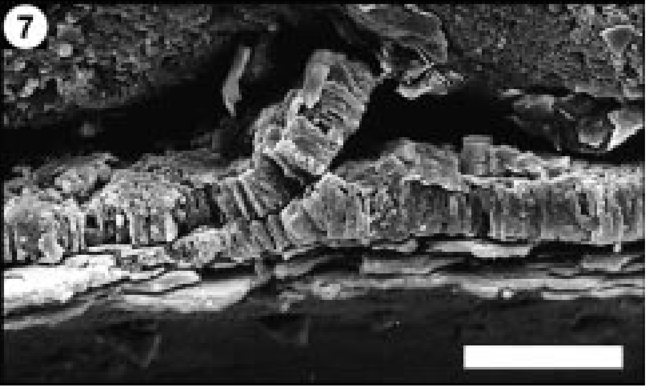
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Plate 5

Fig. 1: Overview of the inner side of a broken protoconch free of matrix of *Kosmoceras* (*Spinikosmoceras*).
c = caecum; p = part of the prosiphon; ps = proseptum; fl = flange with scar of the soft tissue.
Specimen no. MB.C. 3125.
Scale bar = 100 µm.

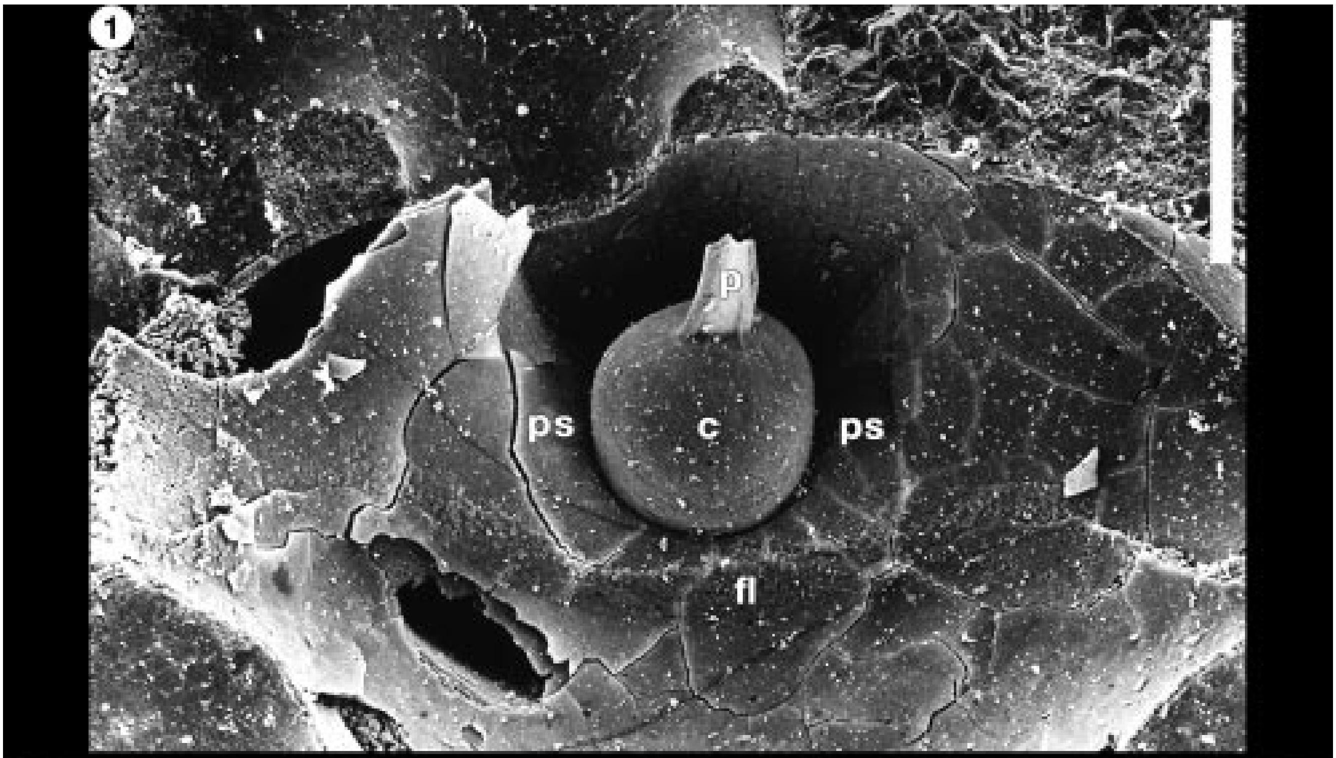
Figs. 2, 3: Caecum of *Kosmoceras* (*Spinikosmoceras*) (same specimen as in Fig. 1) with a preserved part of the prosiphon.
Scale bar = 20 µm.

Fig. 4: Scar of the embryonic soft tissue at the flange (arrow).
Same specimen as in Fig. 1.
Scale bar = 40 µm.

Fig. 5: Attachment zone of the prosiphon with the inner side of the protoconch wall.
Same specimen as in Fig. 1.
Scale bar = 20 µm.

Fig. 6: Part of the protoconch (left side) and of the first whorl (right side) of an ammonitella of *Hecticoceras*, partly filled with pyrite crystals.
The prismatic ultrastructure of the embryonic shell and some internal features are visible.
fl = flange; ps = proseptum; n = first nacroseptum; sf = shell of the first whorl.
Specimen no. MB.C. 3132.
Scale bar = 50 µm.

Fig. 7: Enlargement from Fig. 6 showing the prismatic ultrastructure of proseptum and flange.
Scale bar = 20 µm.


①
p
ps
c
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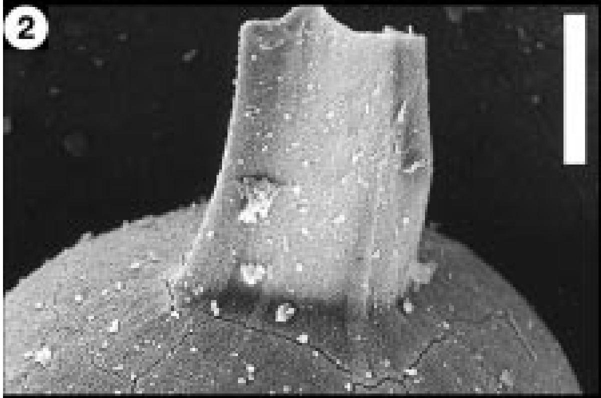
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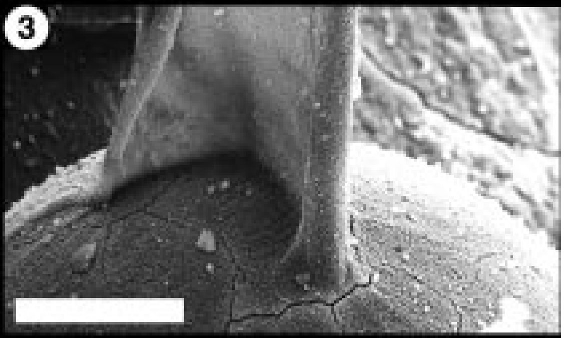
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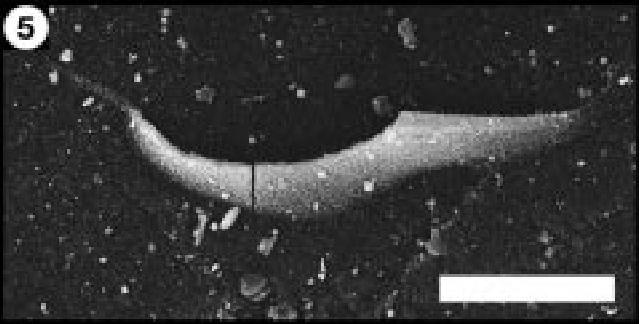
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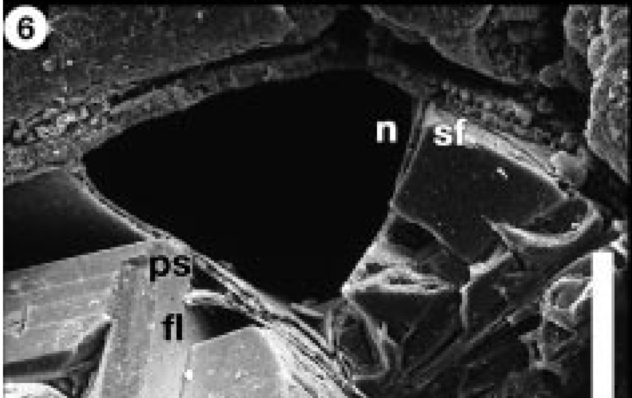
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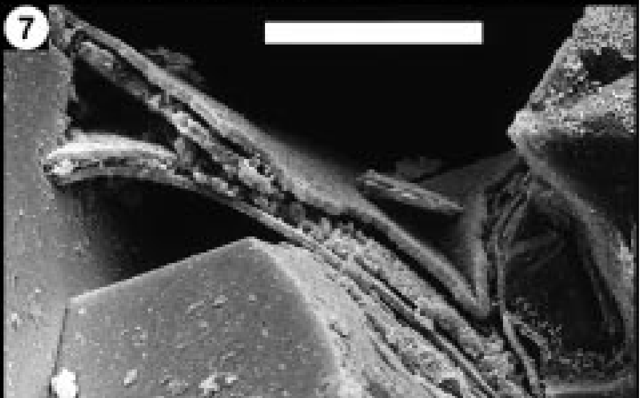
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Plate 6

Fig. 1: Open ammonitella of *Binatisphinctes mosquensis*, partly filled with matrix.
Flange, proseptum and three nacrosepta are clearly visible. The caecum is removed.
fl = flange; ps = proseptum; n = nacrosepta; dw = dorsal protoconch wall.
Specimen no. MB.C. 3111.
Scale bar = 100 µm.

Fig. 2: Enlargement from Fig. 1.
In the centre of the picture there is the flange with an irregular margin. On the left side, the proseptum is visible which shows the same ultrastructure, although there is some diagenetic alteration. On the right side lies the dorsal protoconch wall. Note that the first nacroseptum is considerably thinner than the preceding proseptum.
Scale bar = 20 µm.

Fig. 3: Inner ventral side of the protoconch wall with the complex attachment zone of the prosiphon. Same specimen as in Fig. 1.
Scale bar = 50 µm.

Fig. 4: Caecum of *Binatisphinctes mosquensis* with the attachment zone of the prosiphon (arrow).
Specimen no. MB.C. 3115.
Scale bar = 50 µm.

Fig. 5: Internal mould of the protoconch and a part of the first whorl of *Binatisphinctes mosquensis*.
The suture lines of the proseptum (prosuture) and the nacrosepta are visible.
Specimen no. MB.C. 3120.
Scale bar = 200 µm.

Fig. 6: The ventral part of the proseptum suture line (prosuture) shows a feature resembling the "attachment scar of proseptum", first described in LANDMAN & BANDEL (1985).
Specimen of Fig. 5.
Scale bar = 50 µm.

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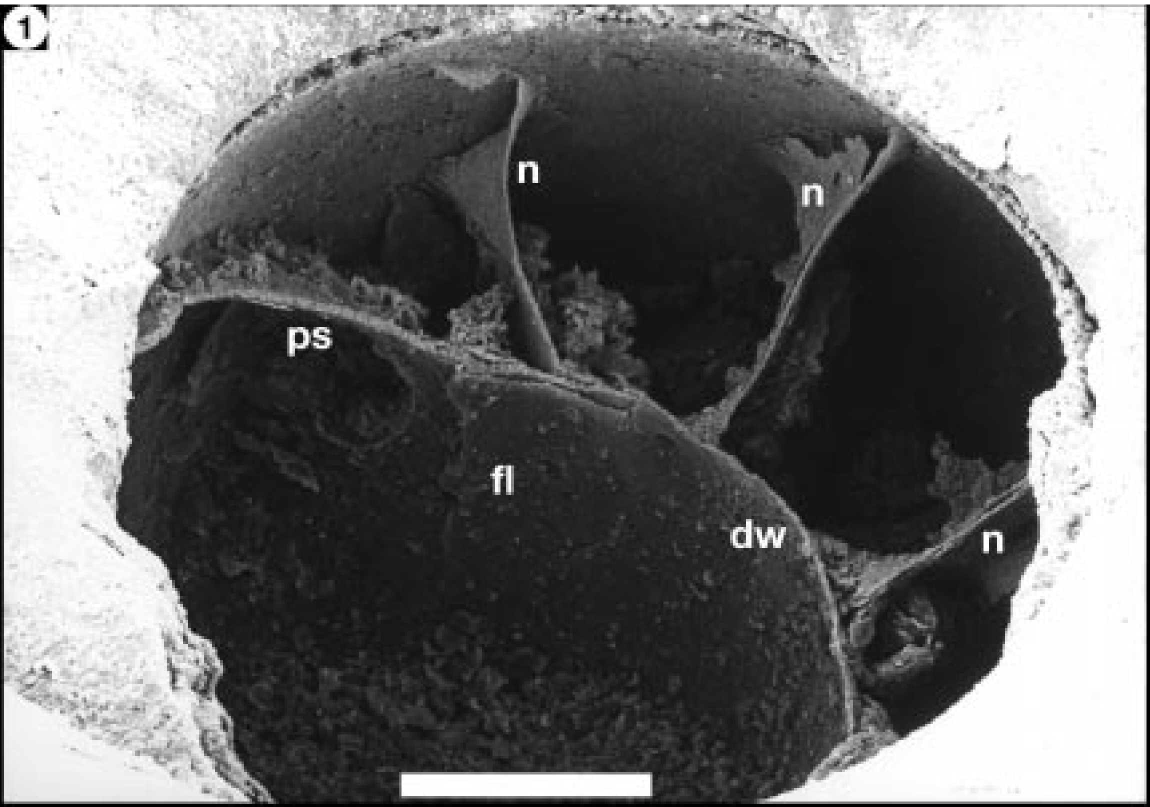

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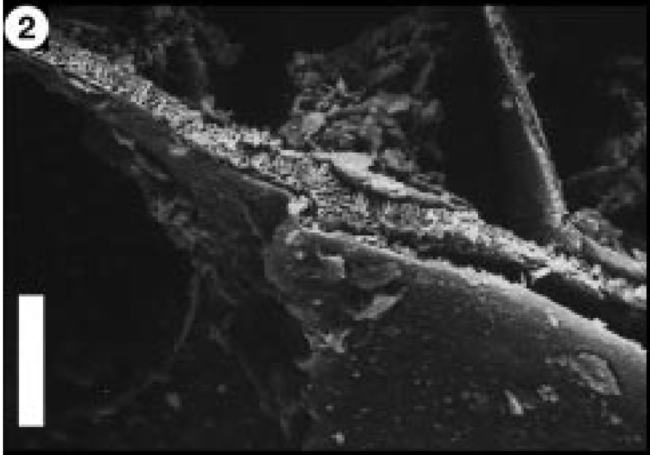

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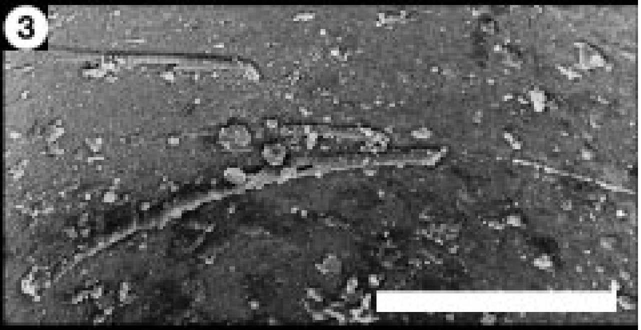

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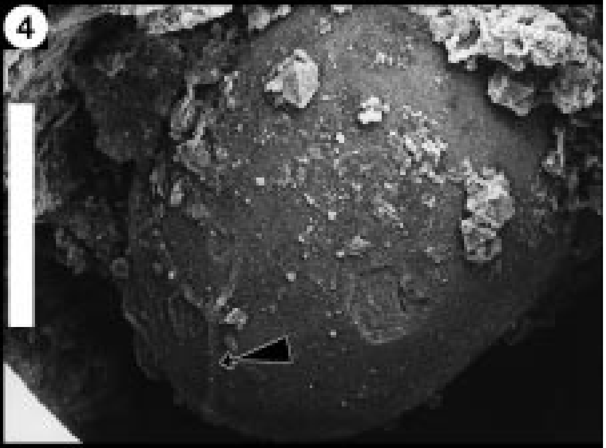

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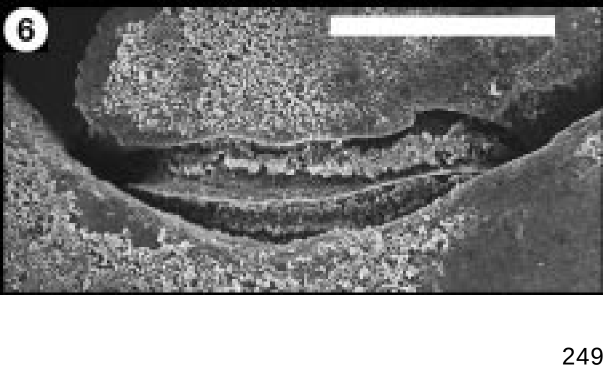


Plate 7

Fig. 1: Ultrastructure of a single tubercle in *Kosmoceras* (*Spinikosmoceras*).
The prismatic crystals building up the tubercle derive from the outer prismatic layer of the ammonitella shell.
Specimen no. MB.C. 3123.
Scale bar = 1 µm.

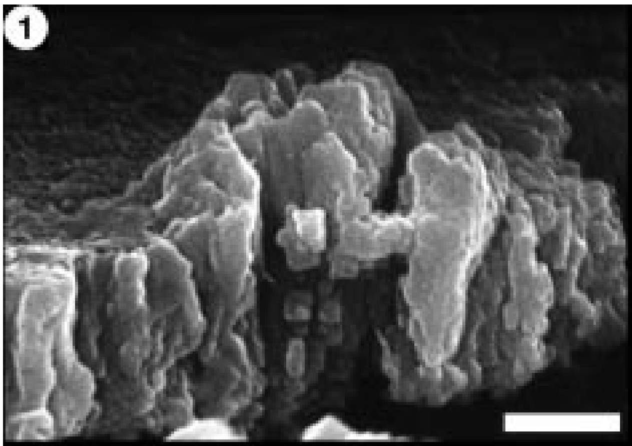
Fig. 2: Tubercles on the ammonitella shell of *Binatisphinctes mosquensis*.
Specimen no. MB.C. 3108.
Scale bar = 20 µm.

Fig. 3: Tubercle distribution on the ammonitella shell of *Binatisphinctes mosquensis*.
The tubercles are spread over the whole umbilicus region. On the lateral or dorsolateral parts of the first whorl, elongated clusters of tubercles are visible. Same specimen as in Fig. 2.
Scale bar = 100 µm.

Fig. 4: Enlargement of Fig. 3.
Scale bar = 50 µm.

Figs. 5–8: Tubercle clusters in other specimens of *Binatisphinctes mosquensis*.
Fig. 5: Specimen no. MB.C. 3116.
Fig. 6: Specimen no. MB.C. 3118.
Fig. 7: Specimen no. MB.C. 3117.
Fig. 8: Specimen no. MB.C. 3119.

Scale bars: Figs. 5, 7: 50 µm; Figs. 6, 8: 20 µm.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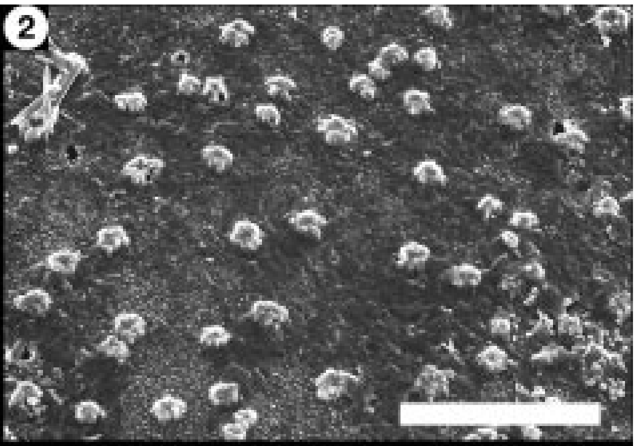
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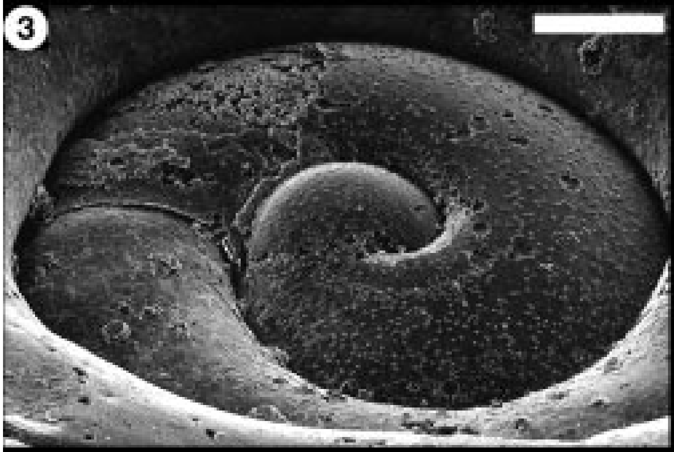
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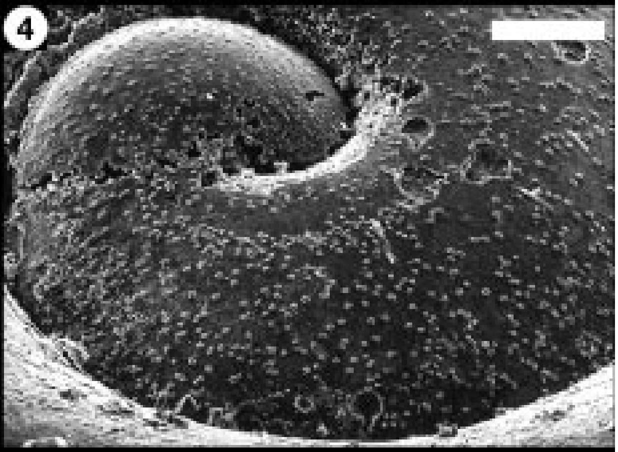
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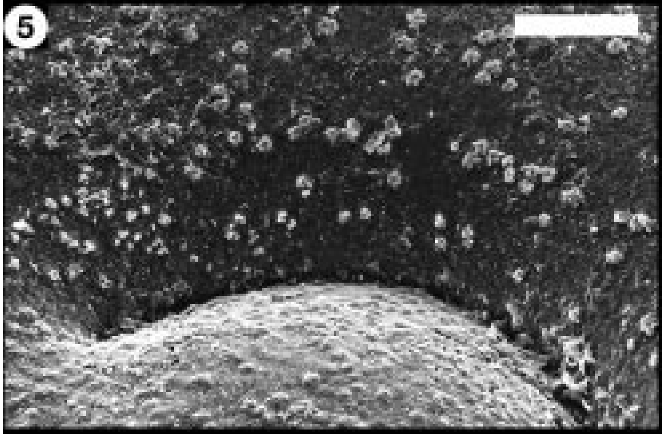
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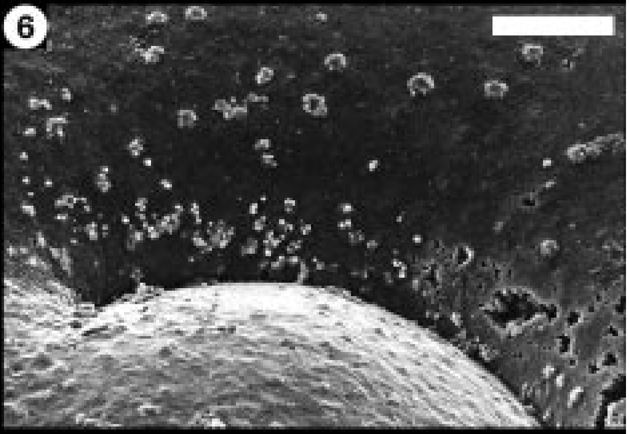
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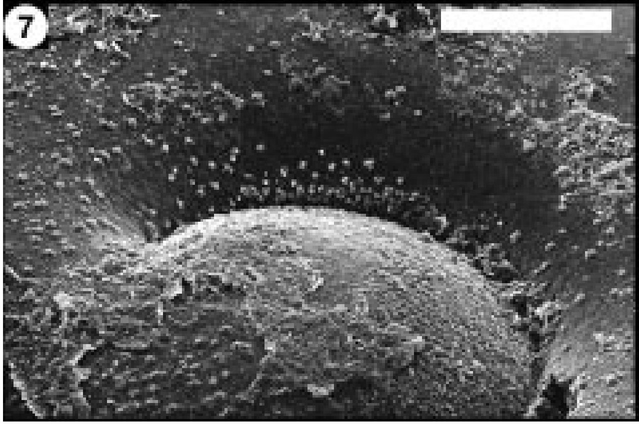
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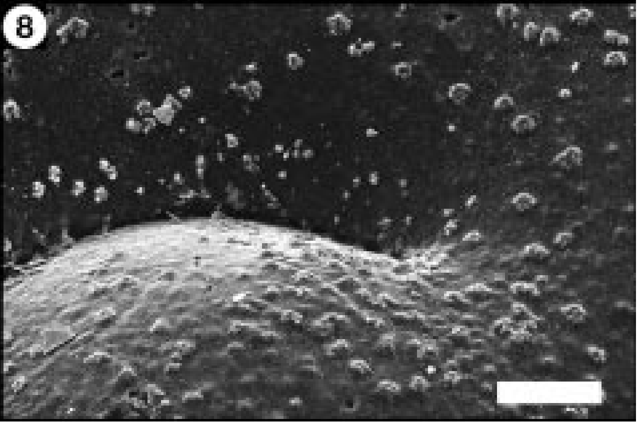
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Plate 8

Fig. 1: Ammonitella in the umbilicus of a *Hecticoceras* conch.
The biggest part of the protoconch and the inner (or dorsolateral) flank of the first whorl before the nepionic constriction are free of tubercles. The other ammonitella shell parts show tuberculate micro-ornament. Tubercles occur more sparsely and are smaller in size in comparison with the other two genera.
Specimen no. MB.C. 3133.
Scale bar = 100 µm.

Fig. 2: Enlargement of Fig. 1.
Tubercles are also present on ventrolateral parts of the shell, which are overgrown by the next, juvenile whorl.
Scale bar = 20 µm.

Fig. 3: Micro-ornament on the juvenile whorls of *Kosmoceras* (*Spinikosmoceras*).
Specimen no. MB.C. 3126.
Scale bar = 200 µm.

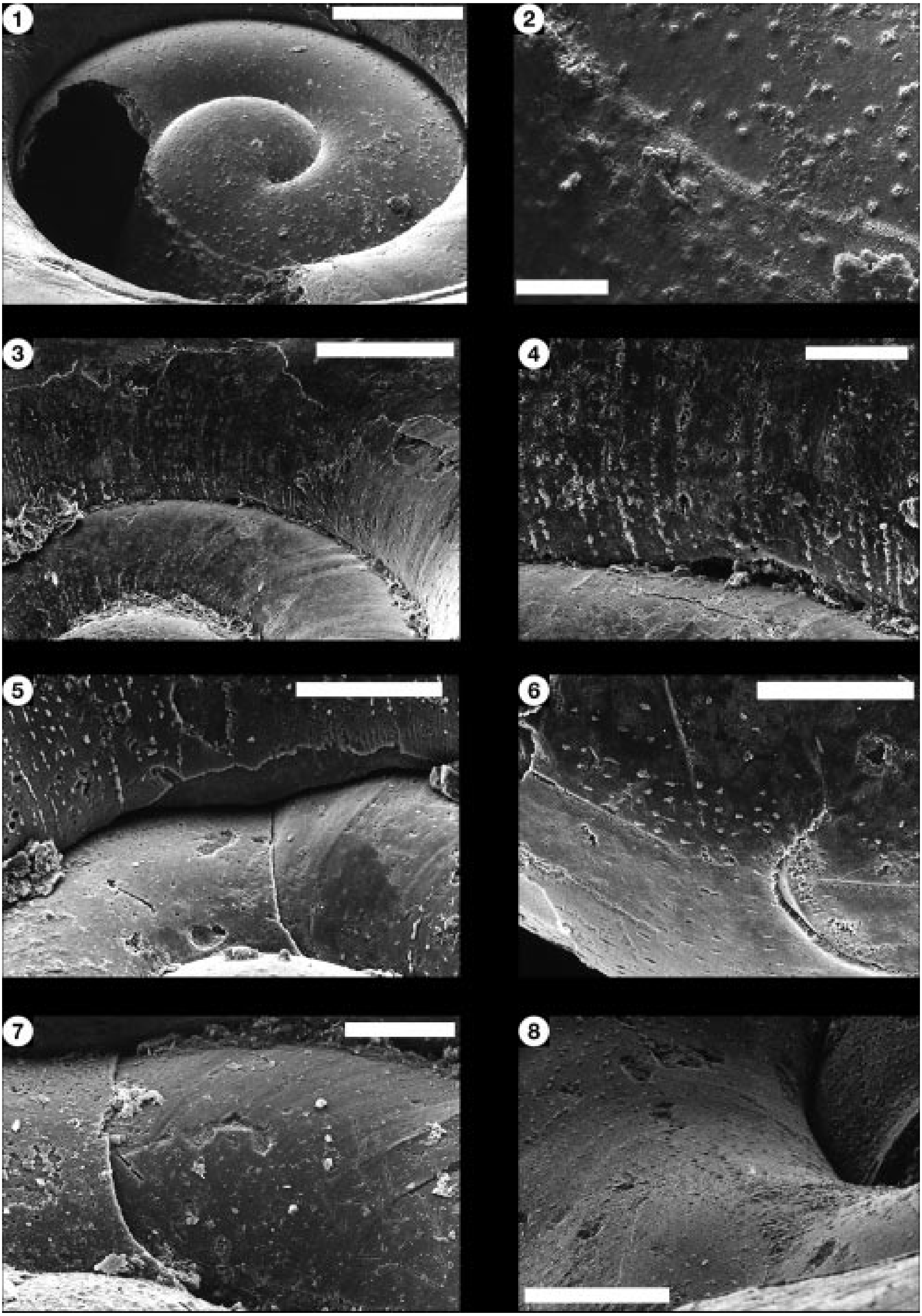
Fig. 4: Enlargement of Fig. 3.
Scale bar = 50 µm.

Fig. 5: Another specimen of *Kosmoceras* (*Spinikosmoceras*).
In the lower part of the picture, the ammonitella edge is visible. On the right side, there is the beginning of the juvenile shell showing growth lines. In the upper part of the picture, there is the next whorl, covered with a tuberculate micro-ornament.
Specimen no. MB.C. 3128.
Scale bar = 100 µm.

Fig. 6: The ventral and lateral parts of the juvenile shell of *Binatisphinctes mosquensis* are also covered by a micro-ornament.
Specimen no. MB.C. 3121.
Scale bar = 100 µm.

Fig. 7: Transition from the ammonitella shell (left) to juvenile shell (right) with projecting growth lines in another *Binatisphinctes mosquensis* specimen.
Specimen no. MB.C. 3112.
Scale bar = 50 µm.

Fig. 8: The juvenile shell of a specimen of *Binatisphinctes mosquensis* is covered with a micro-ornament.
The right side of the picture shows a part of the ammonitella edge.
Specimen of Plate 1, Figs. 1, 2.
Scale bar = 100 µm.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