

DISCUSSION ON MEASURING DIMENSIONAL PARAMETERS OF DEFORMED PLANISPIRALLY COILED LOWER CRETACEOUS AMMONITES (AMMONOIDEA)

DISKUZE K MĚŘENÍ ROZMĚROVÝCH PARAMETRŮ DEFORMOVANÝCH SPIRÁLNĚ VINUTÝCH
SPODNOKŘÍDOVÝCH AMONITŮ (AMMONOIDEA)

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Abstract

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Discussion on measuring dimensional parameters of deformed planispirally coiled Lower Cretaceous ammonites (Ammonoidea).

One of the most important taxonomic features for species determination in undeformed planispirally coiled ammonite shells is the measurement of their size parameters, including shell diameter, whorl height, umbilical width, and whorl width. In Early Cretaceous deposits of Europe, ammonite shells exhibit various types of deformation, as the ammonite-bearing strata primarily consist of clayey-marly limestones. After sediment containing ammonite shells is deposited on the seabed, diagenesis follows. The degree of sediment compaction is controlled by pressure exerted by the height of the overlying water column. Clayey deposits are compressed more than sediments with a predominance of a calcareous component. This process results not only in sediment compaction but also in the planar deformation of ammonite shells. During compaction, the whorl width undergoes substantial changes, rendering its measurement irrelevant for taxonomic purposes. Regions with complex geological structures commonly contain specimens further affected by varying degrees of lateral pressure. The original logarithmic spiral coiling acquires an elliptical shape. This type of deformation partially or even completely alters the original parameters of the ammonite shell. The present contribution, based on an analysis of specifically selected ammonite specimens, demonstrates the consequences of these occurrences. Measurements of shell parameters in specimens deformed by strong lateral pressure are essentially unusable for taxonomic purposes. Such deformation is usually not considered in taxonomic studies of Early Cretaceous ammonites.

Key words: Cephalopoda, ammonite shell, simple deformation, lateral deformation.

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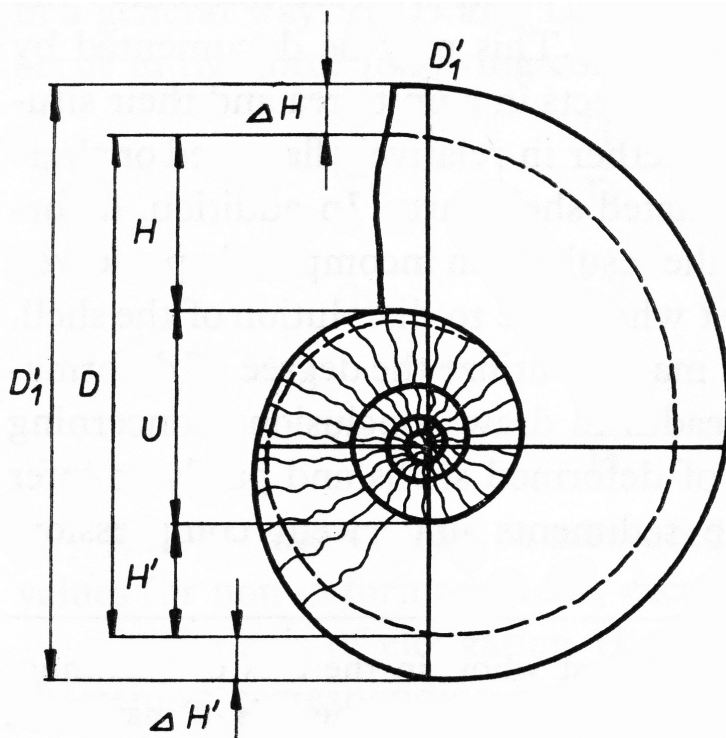
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INTRODUCTION

This paper examines the measurement and evaluation of dimensional parameters in Lower Cretaceous planispirally coiled ammonites, which belong to the category of fossils secondarily affected by later deformation processes. It focuses on specimens preserved in clayey to marly limestones. The study analyses the dimensional parameters of three species

of the genus *Tescheniceras* (VAŠÍČEK 2020) according to collection of REBOULET (1996); three differently deformed specimens identified as *Plesiospitidiscus* cf. *canalis* BUSNARDO *et al.* 2003 (SNM Z 40099, 40100, 41658-9); and one specimen of the genus *Spitidiscus* KILIAN, 1910 (SNM Z 41660).

Undeformed planispirally coiled ammonite shells, which contained the cephalopod body, follow the logarithmic spiral equation (RAUP 1967). The whorls of the shell are bounded by an external and an internal spiral. The external spiral corresponds to the circumference of the shell, whereas the internal spiral defines the base of the whorl. Several simple measurements of the size parameters of the shell (D , H , U , B ; see Text-fig.1) are typically used to describe the style of coiling.



Text-fig. 1: Diagram illustrating changes in the dimensions of the outer spiral of an ammonite shell with the body chamber, caused by deformation due to overburden pressure. The dashed line indicates the outline of the original shell. D - original shell diameter, D'_1 - deformed shell diameter, H - original whorl height, H' - whorl height at the opposite end of the diameter, U - original umbilical width, ΔH - magnitude of whorl height deformation, $\Delta H'$ - magnitude of deformation at the opposite end of the measured diameter.

Text-obr. 1: Diagram změn dimenzí vnější spirály schránky s obývací komůrkou vyvolané nadložním tlakem. Čárkovaná linie indikuje obrys původní schránky. D - průměr původní schránky, D'_1 - průměr schránky po deformaci, H - výška závitů původní schránky, H' - výška závitů na protilehlém konci měřeného průměru, U - šířka umbiliku původní schránky, ΔH - velikost deformace výšky závitů, $\Delta H'$ - velikost deformace na protilehlém konci měřeného průměru.

The most significant primary factor initially influencing the subsequent deformation of an ammonite shell is the difference in its internal structural composition. The initial whorls are reinforced by septa. This part is designated as the phragmocone. The terminal part consists of the body chamber, which contained the soft body of the animal. This part has no reinforcement. The coiling of undeformed shells during the growth of the animal is not constant. It changes slightly during three well-known growth stages of ammonites – juvenile, subadult and adult. The final size of adult ammonite shells is influenced by sexual dimorphism. The smaller shells of male specimens are designated as microconchs (m), while the larger female ones are referred to as macroconchs (M).

Subsequent deformation of original shells can manifest in several forms. The most basic and weakest manifestation of primary deformation is associated solely with pressure effects induced by diagenesis, compaction, and the composition of the sediment overlying the shell lying in the bedding plane. The composition of all components in the bedding sequence of the originally water-saturated sediment is not homogeneous. The percentage values of compaction are not constant. The width of the whorls, compared to whorl height and umbilical width, is deformed to a considerably different degree.

The pressure causing early deformation is perpendicular to the bedding plane and to the shell lying in this plane. However, even the simplest planar deformation may be accompanied by subsequent deformation caused by lateral pressure. The style of such deformation can manifest as either weak or strongly pronounced deformation effects. A clear manifestation of planar lateral deformation is the presence of two visually apparent deformation axes: the shortening axis, in the direction of applied pressure, and the extension axis. The strongest deformation is associated with folding and tectonic activity within the bedding sequence, during which cleavage develops in the axial plane of overturned folds. It manifests as close-joint cleavage and schistosity in the sediment. Such examples of planar shell deformation in Early Cretaceous ammonites have not been extensively documented prior to this study.

Based on the measured values of planarly deformed specimens, particularly those affected by lateral pressure, we aim to characterize and clarify the resulting differences using selected examples of subadult and adult semi-involute shells with overlapping whorls.

METHODS

One of the usual primary requirements in taxonomic processing of planispirally coiled ammonites is measurement of the dimensional parameters of the shell. Ideally, the shell diameter D and other parameters are measured on the corresponding radius, including the whorl width B . Specifically, the diameter $D = H + U + H'$, where H is the whorl height, U is the umbilical width, and H' is the whorl height at the opposite end of the measured radius (see Text-fig. 1). From the measured parameters, the ratios H/D , U/D and B/D are calculated. The first two values objectively express the degree of mutual whorl overlap, whilst B/D characterises the width or cross-section of the whorls. The obtained data with the calculated values are presented in papers describing ammonite species in the measurements section.

During subsequent deformation of original shells, dimensional differences related to ammonite shell construction become apparent, alongside primary growth changes. The differences are also influenced by the places of measuring diameter. Differences in values, albeit small, occur when H and H' are located on the body chamber, or H is on the body chamber but H' is already located on the phragmocone, or H and H' are positioned on the phragmocone. Graphical presentation of measured parameters was provided by e.g. VAŠÍČEK 1972 (fig. 8 or fig. 9 which shows the deformation in umbilicus area).

In the past, with sufficiently measured, well-preserved undeformed ammonite shells, statistical analyses of the above values were published, usually accompanied by their grap-

hical presentation. However, in these contributions, little attention was paid to the effects of deformation. Many published contributions have evaluated primary parameters and other accompanying phenomena related to shell morphology during growth in detail. An overview of these works is provided, for example, by KULLMANN and SCHEUCH (1972), KANT and KULLMANN (1973), BUCHER *et al.* (1996), REBOULET (1996) or MATAMALES-ANDREU and COMPANY (2019).

The ammonite specimens figured here are deposited in the collections of the Slovak National Museum in Bratislava (Slovakia) under deposition numbers with the prefix SNM Z.

RESULTS

Shell Deformed by Overburden Pressure

In this contribution, we present a detailed study of simply deformed ammonite specimens exhibiting a transition from evolute to involute, planarly coiled shell morphologies. The study is based on well-preserved material from the French Early Cretaceous collection compiled by REBOULET (1996) from the Provence Margin and the Vocontian Basin.

Precise measurements of the planarly deformed specimens were conducted on three species belonging to the genus *Tescheniceras*. REBOULET (l. c., p. 44) explained the symbols D, H, and U, which were measured on the body chambers of subadult and adult specimens, as well as similar measurements taken at the end of the phragmocone (marked D, H, U). These symbols are also used in this contribution. However, the exact position of the measurement taken cannot always be determined when the beginning and end of the body chamber are not indicated. During this simple deformation, only the whorl width B changes substantially.

A study on the measurement of individual species by REBOULET (1996) also includes data on apparent differences in values measured on microconchs (m) and macroconchs (M). For our study, we only adopted those measurements from Reboulet that, according to the specimens illustrated by him, are not deformed by lateral pressure. They represent the visually best-preserved individuals of the species *Tescheniceras fluticulum* (THIEULOY 1977), *T. subpachydicranum* (REBOULET 1966), and *T. pachydicranum* (THIEULOY 1977). All adopted measurement data are presented here in Tab. 1. The H/D and U/D values are, as expected, significantly different for each species.

Simply deformed specimens of *T. fluticulum* exhibit a scatter of values across all radii of body chambers: H/D = 0.46 - 0.51; U/D = 0.23 - 0.25. This scatter arises from the fact that it is often not possible to determine whether the measured diameter belongs entirely to the body chamber or whether part of it belongs to the phragmocone. At the end of the phragmocone, H/D = 0.49 - 0.53; U/D = 0.25. The scatter of values observed at the end of the phragmocone is somewhat smaller than that of values measured on the body chamber.

For comparison with the measurements of specimens undeformed by lateral pressure, we also included measurements (Tab. 2) of our sole specimen of *T. fluticulum* (SNM Z 41658) from Podbiel Locality (Pieniny Klippen Belt) illustrated in Pl. 1, Fig. 1. This specimen is strongly deformed by lateral pressure. Notably, in the analysed specimen, the terminal half of the last whorl belongs to the body chamber, while the remainder consists of the phragmocone (see scheme with the symbols of measurement in Text-fig. 3). Measurements along the shortening axis D1, the extension axis D3, and two additional diameters D2 and D4, which form angles of 45° and 135° between both main axes (deflected from the shortening axis) show an unacceptable scatter of H/D and U/D values compared to previous variants. Due to deformation, the final diameter of the shell, which is always the largest in an undeformed specimen, is smaller in the analysed specimen. At the boundary between the body chamber and the phragmocone, there is a notable break (see photo Pl. 1, Fig. 1) on the internal spiral caused by different style of deformation of the phragmocone and body chamber.

A comparison of measured values between studied specimens with deformed shells and undeformed specimens is not possible, as data on the parameters of undeformed shells of *T. fluticulum*, *T. subpachydicranum*, and *T. pachydicranum* were not available.

Shells Deformed by Lateral Pressure

Understanding the consequences of lateral pressure on shell deformation was primarily facilitated by the rich occurrence of ammonites from the group *Plesiospitidiscus cf. canalis* BUSNARDO *et al.* 2003 in the Butkov Quarry (Central Western Carpathians, Slovakia). Besides specimens that are affected only by simple overburden pressure, shells were also found where simple planar deformation was accompanied by deformation induced by unidirectional lateral pressure.

Table 1. *Tescheniceras* - specimens of three species without lateral pressure. Data adopted from REBOULET (1996). Values without underlining H/D and U/D were measured on the body chamber, underlined H/D and U/D at the end of phragmocone.

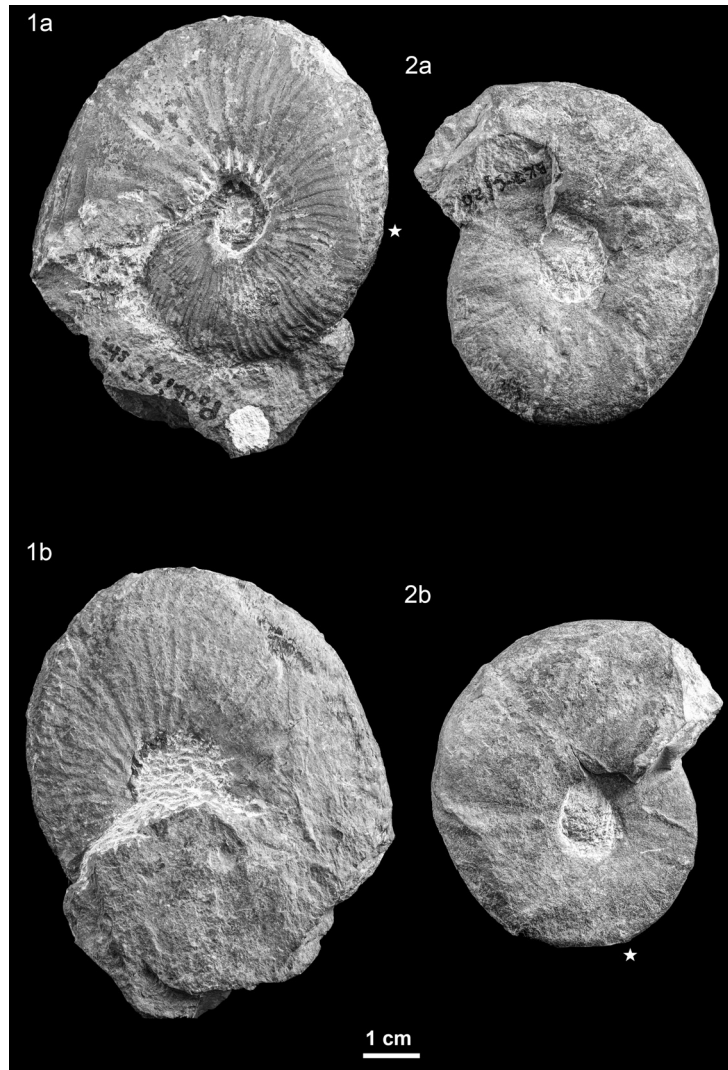
Tabulka 1. *Tescheniceras* - exempláře třech druhů nedeformovaných postranním tlakem. Údaje převzaté z REBOULET (1996). Hodnoty bez podtržení H/D a U/D byly měřeny na obyčvací komůrce, podtržené H/D a U/D na konci fragmokonu.

<i>Tescheniceras flucticulum</i> (Thieuloy, 1977)				
	H/D	U/D	<u>H/D</u>	<u>U/D</u>
Microconchs (D max up to 65 mm)	0.46-0.51	0.23-0.25	0.49-0.53	0.25
Macroconchs (D max 115 mm)	0.45-0.49	0.21-0.26	0.48-0.52	0.22-0.24
<i>Tescheniceras subpachydicranum</i> (Reboulet, 1996)				
	H/D	U/D	<u>H/D</u>	<u>U/D</u>
Microconchs (D max 80 mm)	0.38-0.39	0.33-0.36		
at the end of phragmocone (D max 43 mm)			0.39	0.33-0.34
Macroconchs (D max 120 mm)	0.37-0.39	0.36		
at the end of phragmocone (D max 85 mm)			0.37-0.38	0.34-0.35
<i>Tescheniceras pachydicranum</i> (Thieuloy, 1977)				
	H/D	U/D	<u>H/D</u>	<u>U/D</u>
Microconchs (D max 75 mm)	0.41-0.43	0.29-0.31		
at the end of phragmocone (D approx. 44 mm)			0.44-0.45	0.30-0.31
Macroconchs (D max 145 mm)	0.37	0.33		
at the end of phragmocone (D approx. 105 mm)			0.38	0.32

Table 2. *Tescheniceras flucticulum* (THIEULOY, 1977). Spec. SNM Z 41658, Podbiel Locality. Strong lateral deformation, Pl. 1, Fig. 1.

Tabulka 2. *Tescheniceras flucticulum* (THIEULOY, 1977). Ex. SNM Z 41658, lokalita Podbiel. Silná postranní deformace. Fototab. 1, Obr. 1.

	D ₁	H ₁	U ₁
shortening axis, final end of shell	65.3mm	27.5 (0.42)	13.4 (0.205)
	D ₂	H ₂	U ₂
radius 45°	68.4mm	31.8 (0.46)	14.1 (0.21)
	D ₃	H ₃	U ₃
extension axis	68.6mm	32.5 (0.47)	16.0 (0.23)
	<u>D₄</u>	<u>H₄</u>	<u>U₄</u>
D ₄ - radius 135° on phragmocone	55.0mm	28.3 (0.51)	11.0 (0.20)



Pl. 1, Fig. 1: *Tescheniceras fluticulum* (THIEULOY 1977). Spec. SNM Z 41658, Podbiel Locality, strong lateral deformation, a - right side, b - left side. At the boundary between the body chamber and phragmocone on the internal spiral, there is a break of continuity caused by different style of deformation (see asterisk). Fig. 2: *Plesiospitidiscus* cf. *canalis* Busnardo et al. Spec. SNM Z 41659, Butkov Quarry. Strong lateral deformation, a - right side, b - left side. Boundary between body chamber and phragmocone is marked by asterisks.

Fototab. 1, Obr. 1: *Tescheniceras fluticulum* (THIEULOY 1977). Ex. SNM Z 41658, Podbiel. Silná postranní deformace, a - pravá strana, b - levá strana. Rozhraní mezi obývací komůrkou a fragmokonelem na vnitřní spirále indikuje hvězdička. Obr. 2: *Plesiospitidiscus* cf. *canalis*. Lom Butkov, ex. SNM Z 41659. Silná postranní deformace, a - pravá strana, b - levá strana. Rozhraní mezi obývací komůrkou a fragmokonelem je označena hvězdičkami.

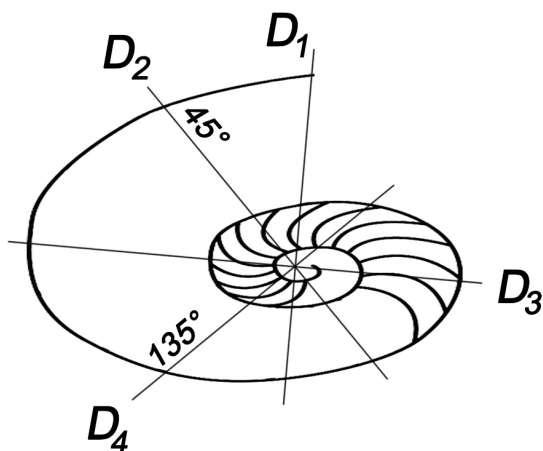
In simply deformed specimens affected only by overburden pressure (e.g., specimen SNM Z 40099, see Text-fig. 2), $H/D = 0.405$ and $U/D = 0.29$ across all measurements taken at any radius of the body chamber. At a diameter of 79 mm, where H was measured on the body chamber, while the opposite H is already located on the phragmocone, $H/D = 0.43$ and $U/D = 0.27$. This difference arises because the body chamber is not reinforced by septa, whereas the phragmocone is.

During lateral pressure deformation, the logarithmic curve of shell coiling acquires an elliptical shape. As mentioned previously, this type of deformation is clearly manifested by two readily apparent principal axes of deformation: the shortening axis D1, which is perpendicular to the prolongation axis (Text-fig. 3). Deformation caused by lateral pressure manifests in either a weaker or stronger form. The terms “weaker” and “stronger” deformation, however, are highly relative concepts. The specific data regarding all possible forms of deformation in *Plesiospitidiscus cf. canalis* are documented in Tab. 3.



Text-fig. 2: *Plesiospitidiscus cf. canalis* BUSNARDO *et al.*, 2003. Spec. SNM Z 40099 deformed by simple overburden pressure. Butkov Quarry, according to VAŠÍČEK and KLEIN (2021).

Text-obr. 2: *Plesiospitidiscus cf. canalis* BUSNARDO *et al.*, 2003. Ex. SNM Z 40099 deformovaný prostým nadložním tlakem. Lom Butkov, podle VAŠÍČKA a KLEINA (2021).



Text-fig. 3: Scheme of measured diameters D of specimens deformed with lateral pressure. D_1 = axis of shortening, D_2 = radian 45° from D_1 , D_3 = axis of extension, D_4 = radian 135° .

Text-obr. 3: Schéma měřených průměrů D exemplářů postižených postranním tlakem. D_1 = osa zkrácení, D_2 = radián 45° , D_3 = osa protažení, D_4 = radián 135° .

Table 3. *Plesiospitidiscus* cf. *canalis*, spec. SNM Z 40100, Butkov Quarry, weak lateral deformation, Pl. 2, Fig. 3. Some value differences are related to occasional imperfect preservation of outline.

Tabulka 3. *Plesiospitidiscus* cf. *canalis*, ex. SNM Z 40100, lom Butkov, slabá postranní deformace. Fototab. 2, Obr. 3. Některé rozdíly v hodnotách jsou spjaté s občasným nedokonalým zachováním obvodu schránky.

	D	H	U
right side	$D_1 = 83.6$	40.0 (0.47)	19.9 (0.24)
left side	$D_1' = 83.6$	34.9 (0.42)	21.4 (0.26)
right side, extension axis	$D_2 = 108.5$	51.4 (0.47)	29.3 (0.27)
left side, D close to max	$D_2' = 108.5$	49.5 (0.44)	27.3 (0.27)
45° - right between main axis	$D_3 = 83$	39.5 (0.48)	19.2 (0.24)
left side	$D_3' = 83$	35.4 (0.43)	21.4 (0.26)
135° - right between main axis	$D_4 = 82.4$	39.6 (0.48)	17.2 (0.21)
135° - left between main axis	$D_4' = 82.4$	39.2 (0.475)	18.4 (0.22)

Table 4. *Plesiospitidiscus* cf. *canalis*, spec. SNM Z 41659, Butkov Quarry, strong lateral deformation, Pl. 1, Fig. 2.

Tabulka 4. *Plesiospitidiscus* cf. *canalis*, ex. SNM Z 41659, lom Butkov, silná postranní deformace, Fototab. 1, Obr. 2.

	D	H	U
right side, end of phragmocone	$D_1 = 48.3$	23.6 (0.49)	10.4 (0.215)
left side	$D_1' = 48.3$	20.0 (0.41)	approx. 11.8 (0.24)
right side	$D_2 = 61.5$	approx. 24.0 (0.39)	approx. 18.0 (0.29)
left side	$D_2' = 61.5$	approx. 29.2 (0.47)	approx. 13.5 (0.22)
between axes 45° , right side	$D_3 = 55.6$	22.0 (0.395)	13.4 (0.24)
left side	$D_3' = 55.6$	28.0 (0.50)	12.5 (0.22)
between 135° , right, ?entire phragmocone	$D_4 = 44.6$	19.5 (0.44)	10.7 (0.24)
left side	$D_4' = 44.6$	18.8 (0.42)	10.9 (0.24)

In the most common variant of lateral pressure, both sides of the shell are affected only to a minor extent. Both sides of the shell show identical morphology. The main axes of deformation manifest as the same on both sides of shell (see Pl. 2, Fig. 3). Based on the measurement results, it follows that H/D values along the prolongation axis are, as expected, considerably higher, while U/D values are lower. Along the shortening axis, these values are relatively close to those measured in specimens undeformed by lateral pressure. During similar measurements along the main deformation axes at a 45° radius, the values differ less markedly than at a 135° radius.

The second case involves strong pressure effects related to the folding of rock units, which particularly lead to the formation of overturned folds. In the axial area of such folds, cleavage along the axial plane develops as a new structural feature. The slip of layers occurs along existing bedding planes, manifesting as pressure-induced close-joint cleavage and schistosity in the rock. Only in very rare cases, when both sides of the shell are preserved, do the main deformation axes of the ammonite lying in the bedding plane on one side exhibits an opposite, mirror-image character compared to the first side.

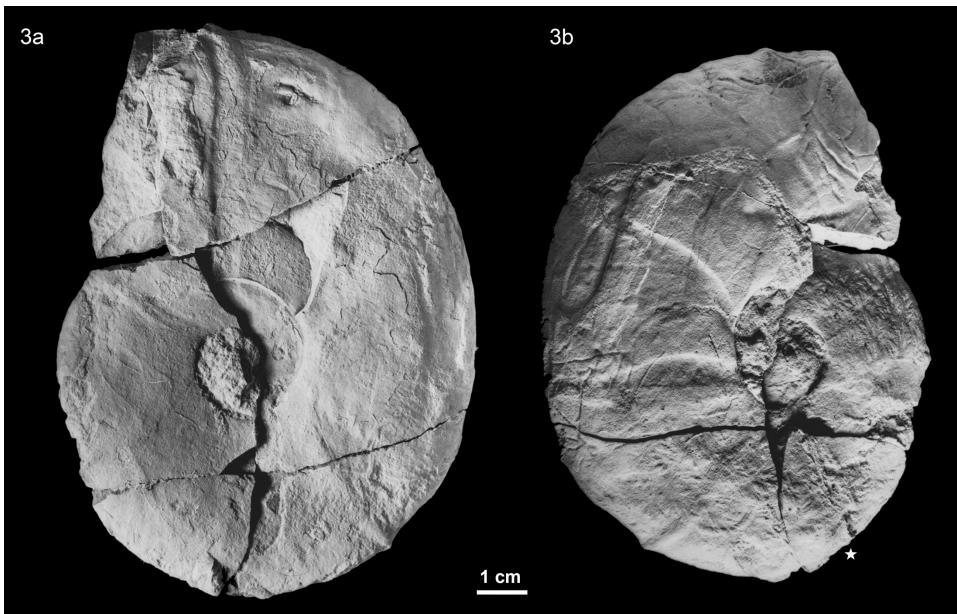
Based on measurements of the only strongly deformed specimen of *Plesiospitidiscus* cf. *canalis* (SNM Z 41658, Pl. 1, Fig. 2) with both preserved sides of the shell, it follows that H/D and U/D values (Tab. 3) differ considerably from those of both simply and weakly deformed specimens affected by lateral pressure. Thus, the conducted measurements have only minimal informational value.

The previous data are further supplemented by a third example of a specimen strongly deformed by lateral pressure, belonging to the genus *Spitidiscus* from the Butkov Quarry (specimen SNM Z 41660), Central Western Carpathians. No specimens with simple deformation or weak lateral pressure deformation were available. Both sides of the illustrated specimen (Pl. 3, Fig. 4), which is not well preserved, appear morphologically quite different. Near the final end on the right side of the shell is the smallest whorl height, H (D approx. 60 mm), corresponding to the shortening axis. On the opposite side, in the same place, which is less favourably preserved, the greatest whorl height is observed (D approx. 70 mm) along the extension axis. Another common feature is the uneven coiling style on both sides of the shell. Only ornamentation could serve for a more precise determination, i.e., a total of eight constrictions on the last half of the whorl and relatively strong, complexly formed ribs in the area on the posterior side of the constrictions. Most ribs originate from umbilical tubercles and cross the venter without interruption.

The degree of deformation depends on where the diameter is measured. The greatest deformation is observed in specimens where the entire measured diameter lies within the body chamber. The deformation is weaker when the diameter is measured initially in the body chamber, with the remaining part on the phragmocone; the weakest deformation occurs when the entire measurement is taken solely on the phragmocone. However, it is not always possible to determine the beginning of the shell or whether the entire measured diameter belongs to the body chamber. The body chamber comprises approximately half of the ultimate whorl.

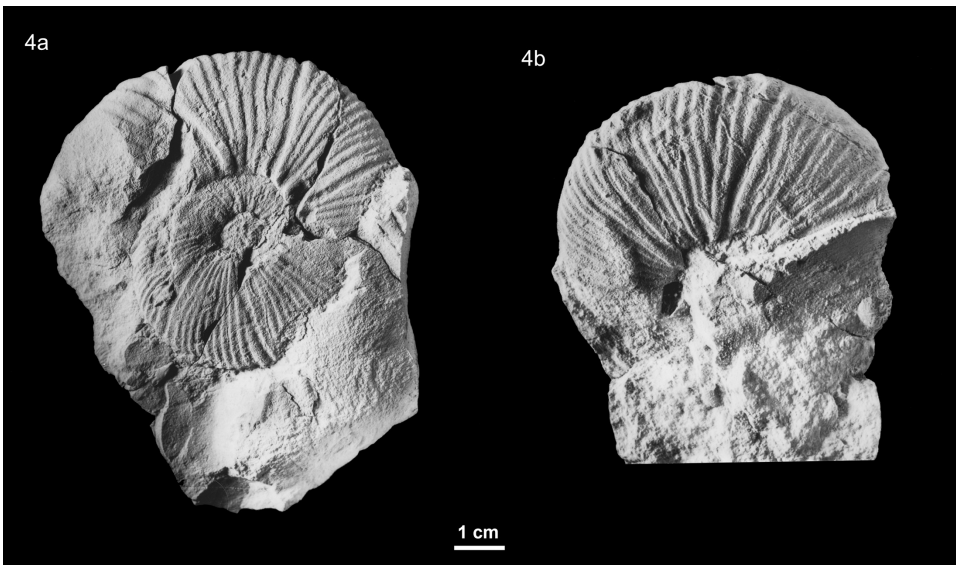
If the deformed shells are ribbed, the shape of the ribs is also deformed (see *Spitidiscus* sp., Pl. 3 Fig. 4). When the direction of lateral pressure aligns with the direction of rib vaulting, the arching of the ribs becomes more pronounced; conversely, when the pressure opposes the vaulting direction, the ribs may appear nearly straight.

This specimen is not unambiguously identifiable; it most likely belongs to the group *Spitidiscus meneghinii* (RODIGHERO 1919). If only one side of the shell were available, species determination would most likely differ for each side.



Pl. 2, Fig. 3: *Plesiospitidiscus* cf. *canalis*. Spec. SNM Z 40100, Butkov Quarry. Weak lateral deformation, a - right side, b - left side.

Fototab. 2, Obr. 3: *Plesiospitidiscus* cf. *canalis*. Spec. SNM Z 40100, Butkov Quarry. Slabá postranní deformace, a - pravá strana, b - levá strana.



Pl. 3, Fig. 4: *Spitidiscus* sp. Spec. SNM Z 41660, Butkov Quarry. Strong lateral deformation, a - right side, b - left side.

Fototab. 3, Obr. 4: *Spitidiscus* sp. Ex. SNM Z 41660, Butkov Quarry. Silná postranní deformace, a - pravá strana, b - levá strana.

DISCUSSION

At ammonite bearing Early Cretaceous localities in the Western Carpathians, undeformed ammonite shells do not occur. The following conclusions can be drawn from the presented results. The most commonly found specimens are those simply deformed by overburden pressure, which acts perpendicular to the shells lying in the bedding plane. Both sides of these specimens exhibit the same morphology. Depending on the degree of applied pressure and the composition of the overlying sediment, the whorl width B on the body chamber is always significantly deformed. The measurement of whorl width is not significant. Parameters H and U are less affected by deformation and remain significant. At all places of measuring diameter D , values of H/D and U/D , remain essentially the same. The exact results are slightly influenced by primary changes related to the growth stages of the ammonite shell and by whether the entire measured diameter D lies within the body chamber or if the opposite height H belongs to the phragmocone. However, this type of deformation, in contrast to the Alpine-Carpathian region, is characteristic for Early Cretaceous ammonites in the Vocontian Basin in France and in related areas with a simple geological structure.

Ammonite deformations are much more complex in European regions with intricate geology, particularly in mountain ranges with an Alpine-Carpathian nappe structure. In addition to the ever-present simple deformation, lateral pressure was also introduced. In ammonite shells, this is expressed by the development of the main shortening axis in the direction of lateral pressure, with the main extension axis forming perpendicular to it. This pressure can vary in intensity, being either weaker or stronger. The weaker variant is characterized by both sides of the shell exhibiting the same coiling style. The main axes on one side of the shell correspond to those on the opposite side. Measured results indicate that H/D values along the extension axis are higher (see Tab. 3) than those along the shortening axis. Along the shortening axis, the measured values are closer to those observed in specimens undeformed by lateral pressure. However, values at other radii differ from those observed in simply deformed specimens.

Strong pressure effects are associated with geological units of nappe structures, where overturned folds occur. In the axial area of these folds, where axial plane cleavage is present, layer slip occurs, leading to the development of close-joint cleavage and rock schistosity. In very rare cases, if both sides of the studied fossil are preserved in thinly cleaved limestone, the main deformation axes on the left side of the specimen are opposite to those on the right side. Values measured at all radii differ so significantly from those of weakly deformed specimens that they are unsuitable for taxonomic determination.

CONCLUSION

A list of possible factors influencing the values of parameters measured on planispirally coiled ammonite shells, based on the examined material, is presented in the Results and Discussion section. The style of deformation is primarily influenced by the fundamental structure of ammonite shells, i.e., the phragmocone and the body chamber, as well as by the varying sizes of adult shells due to sexual dimorphism in ammonites. Additional influencing factors include the location of diameter D measurement. Ideally, measurements should begin at the maximum diameter of the specimen. However, due to the nature of fossilization, the peristome area, i.e., the beginning of the shell or the end of the phragmocone, may not be clearly identifiable. If the end of the phragmocone is also unknown, it remains unclear whether the measured diameter D lies entirely within the body chamber, whether its main part is within the body chamber but extends into the phragmocone, or whether the entire diameter is contained within the phragmocone. The degree of deformation is consistently influenced by the composition of the overlying sediment, particularly by the predominance of clay or calcareous components. This leads to varying degrees of

differences in the measured parameters, which are reflected in the H/D and U/D ratios. The B/D ratio, if measurable at all, is so significantly altered that it becomes taxonomically meaningless.

In deposits with complex geological structures, simply deformed planispirally coiled ammonite shells are also subjected to lateral pressure. Depending on the intensity of pressure, specimens can be categorized as either less affected or significantly affected. In both cases, deformation is characterized by two principal deformation axes: a shortening axis aligned with the direction of lateral pressure and an extension axis perpendicular to it. In less affected specimens, the shortening and extension axes appear symmetrical on both sides of the shell. The H/D and U/D ratios do not differ significantly from those of simply deformed shells.

Strong lateral deformation produces values that deviate markedly from those observed in previous deformation types. It is associated with an additional structural factor affecting the entire rock mass: cleavage. Unfortunately, specimens deformed in this manner are rarely preserved with both sides intact, complicating detailed study. When both shell sides are preserved, the two principal axes on one side are mirror images of those on the opposite side. The measured values deviate significantly from those of less deformed specimens. Measurements of such highly deformed shells do not provide reliable data for species-level taxonomy.

SOUHRN

Jedním z významných taxonomických znaků pro druhovou determinaci nedeformovaných schránek spirálně vinutých amonitů je měření velikostních parametrů schránek D = průměr schránky, H - výška závitů, U - šířka umbiliku, B - šířka závitů (viz obr. 1). Charakter vinutí vyjadřují poměry H/D a U/D . Ve spodnokřídových uloženinách v Evropě se nejčastěji setkáváme se schránkami v různé formě deformovanými, neboť tamější amonitonosné uloženiny reprezentují jílovito-slinité vápence. Po usazení takového sedimentu, na jehož dně leží schránky amonitů, dochází k diagenézi uloženin. Výsledkem je kompakce původně zvodnělého sedimentu. Stupeň kompakce je spojen s tlakem vyvolaným výškou nadložního vodního sloupce, ale také se složením překrývacího sedimentu. Jílovité uloženiny jsou stlačovány více než uloženiny s převahou vápenité složky.

Výsledkem procesu je nejen diagenéze sedimentu, ale také jednoduchá deformace v něm ležících amonitových schránek. Při této deformaci se na obývací komůrce posledního závitů podstatně redukuje šířka závitů B . Její měření nemá význam. Vedle uvedené deformace menší vliv na rozměrové parametry a hodnoty H/D a U/D mají velikostní změny spojené s růstem hlavonožce a s vnitřní stavbou schránky amonitů.

Oblasti se složitou geologickou stavbou běžně obsahují navíc exempláře postižené slabším nebo silnějším postranním tlakem. Způsobená deformace nebývá v taxonomických spodnokřídových publikacích zohledněna. Původní logaritmická spirála vinutí nabývá eliptického tvaru. Dokladem takové deformace jsou vizuálně dobře patrné dvě deformační osy: osa zkrácení ve směru působícího tlaku a na ni kolmá osa protažení.

V případě slabší postranní deformace obě strany schránky mají stejnou morfologii. Hlavní osy deformace po obou stranách si odpovídají. Hodnoty H/D v ose prodloužení jsou oproti stejným hodnotám na nedeformovaných exemplářích značně vyšší, naopak U/D je nižší.

V případě silné postranní deformace v územích s překocnými vrásami vzniká jako nový strukturální prvek kliváž osní roviny. Dochází k prokluzu vrstev podle stávajících vrstevních ploch. Projevuje se to zbrídlíčením horniny. Hlavní osy deformace amonita ležícího v takové vrstevní ploše na straně jedné mají opačný, tj. zrcadlově odlišný charakter než na straně protilehlé. Vypočtené poměry H/D a U/D jsou v podstatě pro taxonomii neupřítelné.

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REFERENCES

- BUCHER, H., LANDMAN, N. H., KLOFAK, S. M., GUEX, J., 1996: Mode and Rate of Growth in Ammonoids. – In N. H. LANDMAN, K. TANABE, R. A. DAVIS (Eds): *Ammonoid Paleobiology*, 13, 407–539. Plenum Press, New York.
- BUSNARDO, R., CHAROLLAIS, J.-J., WEIDMANN, M. CLAVEL, B., 2003: Le Crétacé inférieur de la Veveyse de Châtel (Ultrasubalpines des Préalpes externes; canton de Fribourg, Suisse). – *Rev. Paléobiol.*, 22, 1–174.
- KANT, R., KULLMANN, J., 1973: “Knickpunkte” im allometrischen Wachstum von Cephalopoden-Gehäusen. “Inflexion points” the allometric growth of cephalopod shells. – *N. Jb. Geol. Paläont. Abh.*, 142, 97–114.
- KULLMANN, J., SCHEUCH, J., 1972: Absolutes und relatives Wachstum bei Ammonoideen (Konstruktions-Morphologie Nr. 5). – *Lethaia*, 5, 129–146.
- KILIAN, W., 1910: Erste Abteilung: Unterkreide (Palaeocretacicum), Lieferung 2 – Das bathyale Palaeocretacicum im südlichen Frankreich; Valendis-Stufe, Hauterive-Stufe, Barreme-Stufe, Apt-Stufe. – In F. FRECH *Lethaea Geognostica. II Das Mesozoikum, Band 3 (Kreide), (1907–1913)*, 169–288. Schweizerbart, Stuttgart.
- MATAMALES-ANDREU, R., COMPANY, M., 2019: Morphological variability patterns in the *Balearites-Pseudothurmannia* genera boundary (Ammonoidea, late Hauterivian): taxonomical and biostratigraphic implications. – *Journ. Syst. Palaeont.*, 17 (13), 869–895.
- RAUP, D. M., 1967: Geometric analysis of shell coiling: coiling in ammonoids. – *Journ. Paleont.*, 41, 43–65.
- REBOULET, S., 1996: L'évolution des ammonites du Valanginien-Hauterivien inférieur du bassin vocontien et de la plateforme provençale (Sud-Est de la France): relations avec la stratigraphie séquentielle et implications biostratigraphiques. – *Doc. Lab. Géol. Fac. Sci. Lyon*, 137 (1995), 1–371.
- RODIGHERO, A., 1919: Il sistema cretaceo del Veneto occidentale compreso fra l'Adige e il Piave, con speciale riguardo al Neocomiano dei Sette Comuni. – *Palaeontogr. ital.*, 25, 39–125.
- THIEULOY, J.-P., 1977: La zone à *callidiscus* du Valanginien supérieur vocontien (Sud-Est de la France). Lithostratigraphie, ammonitofaune, limite Valanginien-Hauterivien, correlations. – *Géol. Alp.*, 53, 83–143.
- VASÍČEK, Z., 1972: Ammonoidea of the Těšín-Hradiště Formation (Lower Cretaceous) in the Moravskoslezské Beskydy Mts. – *Rozpr. Ústř. Úst. geol.*, 38, 1–103.
- VASÍČEK, Z., 2020: *Teschenceras* gen. nov. (Ammonoidea) and the definition of the Valanginian/Hauterivian boundary in Butkov Quarry (Central Western Carpathians, Slovakia). – *Acta geol. pol.*, 70, 569–584.
- VASÍČEK, Z., KLEIN, J., 2021: On imperfectly known Hauterivian representatives of the families Holcodiscidae Spath, 1923 and Barremitidae Breskovski, 1977 in Butkov Quarry (Central Western Carpathians, Slovakia). – *Acta geol. pol.*, 71, 433–451.