Orientation of *Spondylus* valves cemented to the hard-rock substrates (Bivalvia, Upper Cretaceous, Bohemia)

Orientace misek rodu *Spondylus*, přitmelených k pevným horninovým substrátům (Bivalvia, svrchní křída, Čechy) (Czech summary)

(6 text-figs., 4 plates)

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Data on orientation of *Spondylus* sp.encrusting the rocky bottom and boulders in the nearshore facies (upper Cenomanian-lower Turonian, Bohemian Cretaceous Basin) are summarized and compared with those on encrusting bivalve *Atreta*. While the subhorizontal rocky surfaces bear both *Spondylus* sp. and *Atreta* orientated chaotically, on sloping substrates (the dip equal to or exceeding 10°) they are usually orientated preferentially, i.e., umbos of valves are directed to the upper left quadrant (so-called slope orientation). In agreement with Seilacher (1960) we tentatively consider this posture to be advantageous for nutrition and providing other biological functions. Most recently, a modified orientation of *Spondylus* was found on the overhanging roof of a small cavity, sheltered from the exterior by a clast barrier. The *Spondylus* valves are here mostly directed to the lower left quadrant by their umbos. It means that, under the local conditions, the posterior margins of valves were turned to the barrier, through which the cavity communicated with the exterior water environment. A fragment of an irregular cluster with partial radial orientation of *Spondylus* valves was also found on another substrate of the same locality (Skalka near Velim, central Bohemia). Several extra-Bohemian examples of Mesozoic encrusters are discussed.

Introduction

From the Bohemian Cretaceous Basin (BCB), the spondylids encrusting hard-rock substrates (mostly clasts) have been known for a rather long time (see Frič 1870, 1910, Culek 1944, Zázvorka 1946, Klein 1962, Soukup 1966, Bouček 1968, Macák et al. 1968, Ziegler 1982). Unpublished observations are also frequent (see table 1). Fauna encrusting the rocky bottom and large boulders which both occur in the nearshore facies, was, however, intensively studied only during the last few years (Houša - Nekvasilová 1984, Nekvasilová - Žítt 1988, Žítt - Nekvasilová 1989, 1990, 1991, 1992, 1993, Žítt 1992). The bivalve *Spondylus* sp. was ascertained to be relatively frequent in the studied communities. Most recently, the authors found new rocky surfaces colonized by these bivalves which are so far the richest in number of specimens per area measured and which provided new interesting information on their distribution and orientation. As a result, all the data on cemented *Spondylus* sp. are summarized from the BCB, and this bivalve growth orientations are compared with those of *Atreta* in search for preferred orientation causes.

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Geology, substrates, localities

Localities of the studied encrusters are situated in the Korycany Member of the Peruc-Korycany Formation and in the basal parts of the overlying Bílá Hora Formation. Korycany Member consists mostly of conglomerates (containing gneiss or silicite clasts at the studied localities), usually clast supported, very coarse and unsorted, with lithologically complicated but prevailingly limestone-claystone matrix. They are of upper Cenomanian age. The base of the lower Turonian Bílá Hora Formation is formed mostly by clayey-silty sediments which pass upwards into siltstones with sponges. There exists a hiatus between the mentioned formations, spanning probably the uppermost Cenomanian. During this interval, sedimentation rate rapidly decreased and phosphogenesis occurred followed by a period of reworking (see Žítt - Mikuláš 1994). At the studied localities, the sediments of both units usually fill the depressions eroded in the rocky bottom by transgressing Cenomanian sea (see pls. I and III).

Though *Spondylus* encrusts several types of hard substrates in the BCB (such as the bioclasts, rock - clasts, and rocky bottom), only the specimens from the rocky bottom, and from rock clasts undisturbed in their position since their encrustation till now, are included in this paper. Basic data on all known localities, types of substrates and partly on the number of encrusting specimens are summarized in table 1. As regards a detailed information on the Radim locality, we refer to Žítt (1992). Localities of Kutná Hora-Karlov and Líbeznice were described by Nekvasilová - Žítt (1988) and Žítt - Nekvasilová (1992), respectively. New instructive occurrence of encrusting *Spondylus* and other fauna were recently found at the locality Skalka near Velim (about 6 km west of Kolín, central Bohemia). Here, several erosional troughs cutting a low gneiss elevation are exposed in a small abandoned quarry. Most important are two large depressions located in the western (see pl. III, fig. 1, and Nekvasilová 1986, fig. 2) and a small one in the eastern parts of the quarry (see pl. I, fig. 1).

Encrusting communities

In the paper by Žítt - Nekvasilová (1993) a preliminary concept of two successive encrusting communities was introduced. The older community is characterized by

Table 1
Distribution of *Spondylus* sp. cemented to the hard-rock substrates in the nearshore facies (BCB, upper Cenomanian-lower Turonian)

Locality	Spondylids found in					Determination	Authors
	Oyster community		Atreta-Bdelloidina community				
	cl. r.	r. b.	cl. i. s.	cl. r.	r. b.		
Chrtníky	-	-	1	S?	-	Spondylus sp.	Žítt - Nekvasilová (1991)
	-	-	-	+	-	S. hystrix	Zázvorka (1946)
Kojetice	+(?)	-	-	-	-	Spondylus	Frič (1910)
Kutná Hora-Karlov	-	-	>50	S?	-	Spondylus sp.	Nekvasilová - Žítt (1988)
	-	-	>51	S?	-	Spondylus sp.	Žítt - Nekvasilová (1989)
Kutná Hora - Na Vrších	+	-	-	-	-	Spondylus	Bouček (1968)
	+	-	-	-	-	spondyli valves	Macák et al. (1968)
Líbeznice	-	-	-	+	21	Spondylus sp.	Žítt - Nekvasilová (1992)
Mezholezy	+(?)	-	-	-	-	valves of Spondylus	Klein (1962)
Nová Ves near Kolín	-	-	-	1	-	Spondylus sp.	O. Nekvasilová - field observation 1990
Odolena Voda	-	-	-	1	-	Spondylus sp.	Hradecká - Nekvasilová - Žítt (in print)
Plaňany	-	+	-	-	-	Spondylus	Soukup (1966)
Předboj (close to road)	+(?)	-	-	-	-	Spondylus sp.	O. Nekvasilová (unpublished data)
Radim	+	-	-	-	-	Spondylus lineatus	Ziegler (1982)
	1(?)	-	-	-	20	Spondylus sp.	Žítt (1992)
Skalka near Velim							
site No. 1.	-	-	-	-	2	Spondylus sp.	This paper
site No. 2	-	-	-	-	1	Spondylus sp.	O. Nekvasilová - field observation 1965; this paper
site No. 3	-	6	-	-	-	Spondylus sp.	This paper
site No. 4	-	-	-	-	82	Spondylus sp.	This paper
Skalka near Žehušice	-	-	-	-	+	Spondylus sp.	Culek (1944)
	-	-	-	-	1	Spondylus sp.	O. Nekvasilová - field observation 1982
Středokluky	-	-	-	-	9	Spondylus sp. (slope orient.)	O. Nekvasilová - field observation 1966
	-	-	-	-	+	Spondylus sp.	Klein - personal communication 1989
Tuchoměřice - Kněžívka	1	-	-	-	-	Spondylus sp.	Žítt - Nekvasilová (1990)
Zbyslav	-	-	-	-	+	Spondylus shells	Frič (1870)

cl. r. - encrusted and then redeposited clasts, cl. i. s. - clasts preserved in undisturbed position since their encrustation, r. b. - rocky bottom, + - number of specimens not recorded, +(?) - number of specimens not recorded and community type uncertain, S(?) - remains of *Spondylus* affinity (bad preservation) oysters [*Exogyra reticulata* Reuss, *Exogyra haliotoidea* (Sowerby), a. o.], the younger one by the bivalve *Atreta* (two species) and the agglutinated foraminifera *Bdelloidina cribrosa* (Reuss). The first community was replaced by the second when the coarse accumulations of the Korycany Member became stable and sedimentation rate rapidly decreased prior to a phosphogenic episode. The *Atreta*-*Bdelloidina* community survived not only during the breaks in phosphogenesis when the supposed anoxy of the environment was temporarily decreasing, but also after the phosphogenesis, under the fully oxic conditions at the beginning of the lower Turonian sedimentation. *Spondylus* sp. formed a part of both oyster, and *Atreta-Bdelloidina* communities. Attribution of the studied bivalves to the respective community types is specified in table 1.

General notes to *Spondylus*

The genus *Spondylus* Linné, 1758 belongs to the family *Spondylidae* Gray, 1826 of pectinacean bivalves. Its right valves are slightly inequilateral, pectiniform (see Hertlein - Cox 1969). In our material they are low and attached to the hard-rock substrate by the whole surface. Left valves were never found in situ by the present authors. Attachment of some specimens on the walls of very narrow crevices, however, suggests their relatively low height. Radial costae but no apparent muscle scars are present in the interiors of the cemented valves. Hinge parts are mostly badly preserved.

In the sediments of the upper Cenomanian-lower Turonian of Bohemia three species of *Spondylus* were

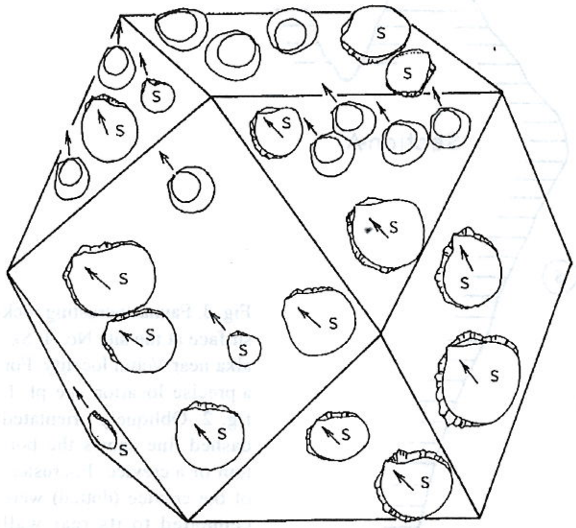

Fig. 1. Distribution and orientation of *Spondylus* and *Atreta* valves on variously inclined surfaces of a polyhedron (scheme of sphalerite crystal as an example). Note the top plane (horizontal) where *Atreta* is more frequent than *Spondylus* but both are chaotically orientated. On inclined or vertical planes, they have a preferred slope orientation. *Atreta* is rare on vertical, and absent from the overhanging surfaces. S - *Spondylus*, not marked-*Atreta*. Not in scale

distinguished by Reuss (1845), Frič (1911) and other workers. These are *S. lineatus* Goldfuss (= *S. latus* Sowerby according to Frič, op. cit.), *S. striatus* Sowerby, and *S. hystrix* Goldfuss. Small fragments of left *Spondylus* valves found by ourselves in the sediments surrounding the encrusted rock substrates were, however, difficult to determine, as well as the in situ preserved right valves. For that reason, we use only the *Spondylus* sp. designation for our specimens. Careful taxonomic revision of the above mentioned spondylid species from the BCB is, in our opinion, a prerequisite to more precise determinations.

Orientation of cemented valves on the substrate

In the BCB, the first observation of *Spondylus* orientations on the rocky surfaces was made by Soukup (1966) at the Plaňany locality in central Bohemia (substrates later destroyed by quarrying). Except for the statement of orientated attachment to the rock, no other details were, however, given by this author. First more precise information from the BCB was published by Nekvasilová - Žítt (1988) from the Karlov locality. Considering those and all the other so far gathered data, the orientations of *Spondylus* sp. may be summarized into the following three groups:

1. Orientations on horizontal surfaces

At the studied localities, strictly horizontal rock surfaces are scarce. However, on subhorizontal substrates (of about 5° dip angle), both *Spondylus* and *Atreta* were observed in chaotic orientations (see pl. IV, fig. 5). While *Spondylus* is very rare here, *Atreta* is common and shows the same density as in populations on steeper slopes (see below).

2. " Slope orientation" on inclined surfaces

At Karlov locality, *Spondylus* sp. formed a part of a community encrusting a large gneiss boulder of the uppermost part of the conglomerate accumulation, immediately overlaid by claystones of the Bílá Hora Formation. On slopes of minimum dip angle of ca. 10°, both *Spondylus* and *Atreta* orientate themselves preferentially, their cemented valves directed by the umbonal parts to the upper left quadrant (see pl. IV, figs. 3, 4, text-fig. 2). It is necessary to note, however, that this orientation does not originate as a response to the general slope of the substrate, but rather as a reaction to its strictly local position. For example, we can see a roughly rugged sloping surface with several specimens orientated in other and sometimes even opposite directions. However, a detailed inspection shows that every *Atreta* and *Spondylus* is orientated adequately to the local dip. On flat smooth slopes the orientation is mostly uniform.

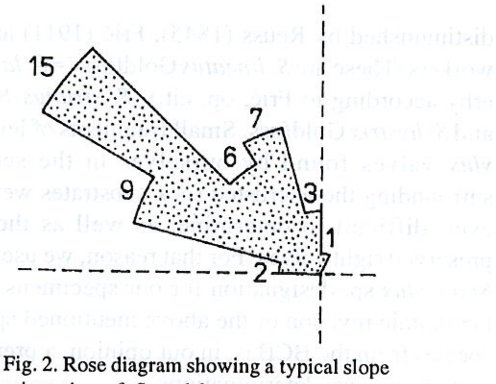

Fig. 2. Rose diagram showing a typical slope orientation of *Spondylus* sp. valves, measured on a gneiss boulder from the Kutná Hora-Karlov locality. One sector equals to 15°, one specimen = 4 mm. Number of specimens per sector is marked. N = 43

This orientation of *Atreta* and *Spondylus* on slopes was, until the present, confirmed several times in the BCB. In accordance with Seilacher (1960), we designated it as the slope orientation (Žítt - Nekvasilová 1991, 1992, Žítt 1992). Orientations of *Dimyodon nilssoni* (Hagenow) on the steep walls of highly convex echinoid tests from the north German Upper Cretaceous (see Schmid 1949, Nestler 1965, Müller 1969, Kutscher 1971) correspond well with the above mentioned slope orientation of the Bohemian *Atreta* on the rock substrates. The identity or at least a close affinity of *D. nilssoni* to our *Atreta* sp. 2 (sensu Nekvasilová - Žítt 1988) seems to be, after all, highly probable.

Spondylus is a little different from *Atreta* in its relation to the overhanging surfaces. While we never found *Atreta* cemented to the overhangs (and it is very rare on vertical surfaces), *Spondylus* encrusts them commonly (see text-fig. 1). This corresponds well with the observation of Lescinsky et al. (1991, p. 137) that "spondylids are one of the few bivalves cemented to overhangs ".

Measurements of *Spondylus* orientations (see rose diagram on text-fig. 2) on very steep, vertical, and overhanging surfaces of the Karlov boulder (see Nekvasilová - Žítt 1988) showed that the position of substrate in no case substantially affected them. Identical slope orientations of *Spondylus* were found on the rocky bottom of the Radim locality (Žítt 1992, pl. II, fig. 1; pl. IV, figs. 1, 2). At the Líbeznice locality, the orientations were the same both on the oblique, vertical, and overhanging silicite-rock surfaces. The majority of *Spondylus* valves occurred here, however, on boulders, the undisturbed position of which was uncertain (see Žítt - Nekvasilová 1992, fig. 7, and here pl. IV, fig. 2). *Spondylus* sp. in slope orientation was formerly found

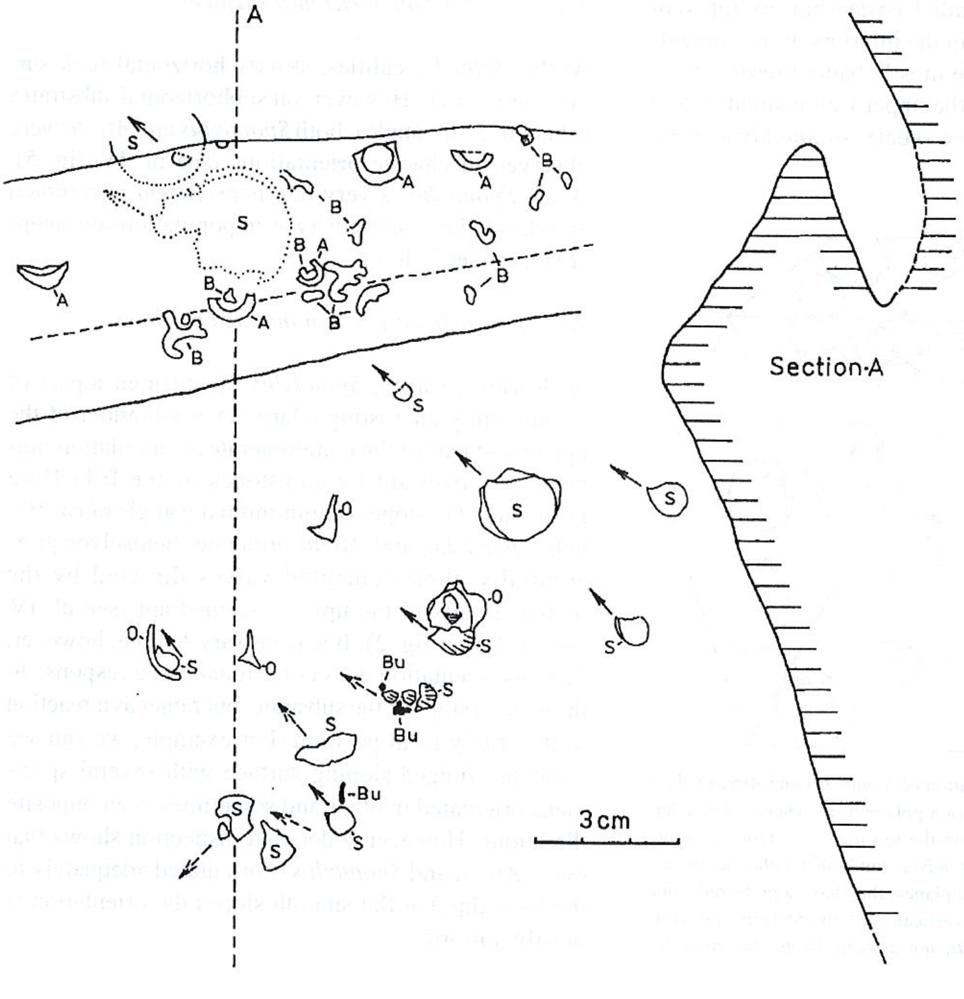

Fig. 3. Fauna encrusting rock surface at the site No. 4, Skalka near Velim locality. For a precise location see pl. I, fig. 2. Obliquely orientated dashed line shows the bottom of a crevice. Encrusters of the crevice (dotted) were cemented to its rear wall (dashed in the section on the right). A - *Atreta*, B - *Bdelloidina*, Bu - *Bullopora*, O - indetermined oyster, S - *Spondylus*. Note that *Atreta* and *Bdellodina* are missing on the overhangs

also at the Skalka near Velim locality. Here, specimens rarely encrusted the steep rock walls of depressions called Václav and Veronika in the western part of the quarry (see sites Nos. 1 and 2 in table 1 and on pl. III, fig. 1).

3. *Different orientations on inclined surfaces*

Until now we presented here a rather uniform orientation pattern of our *Spondylus* specimens on the oblique, vertical and overhanging rock surfaces. Different orientations were found to be highly exceptional on our substrates (one specimen at the Radim locality - see pl. IV, fig. 1, one specimen at the Kutná Hora-Karlov locality). The break-through into this "obligatory" scheme of orientations on inclined substrates was made only due to the most recent finds at the Skalka near Velim locality (sites Nos. 3 and 4).

Spondylus sp. observed at site No.3 (see table 1 and pl. III, fig. 2) formed an interesting colony, which was, unfortunately, only fragmentarily preserved. Some specimens are orientated approximatelly radially, thus resembling those described by Surlyk - Christensen (1974) from the Swedish Upper Cretaceous. Colonized rock is very steep (about 60-70°), morphologically simple and deeply buried by the conglomerate filling of the depression (Veronika depression). Most important is, however, the site No. 4 located in the eastern part of the quarry, on the wall of a shallow depression, where the encrusted rock parts are covered by uppermost clasts of the conglomerate accumulation and by the overlying claystones (see pl. I, figs. 1, 2). Rock substrate highly varies morphologically, being erosively shaped into the deep and long crevices with ledges in between, and with many overhanging parts (local profiles see text-figs. 3 and 4). Text-figures 3, 4, and 5 show the valves of *Spondylus* on the overhangs and, in part, on vertical surface (text-fig. 4). While on the substrates in figs. 3 and 4 they have, with one exception, a typical slope orientation (see the rose diagram in text-fig. 4), the overhang in text-fig. 5 displays orientations rather different. We can see that the majority of valves is orientated by their umbonal parts subhorizontally or down to the left (see the rose diagram in text-fig. 5). We have ascertained here at least three generations of *Spondylus* specimens, which do not differ substantially in the position of their growth axes.

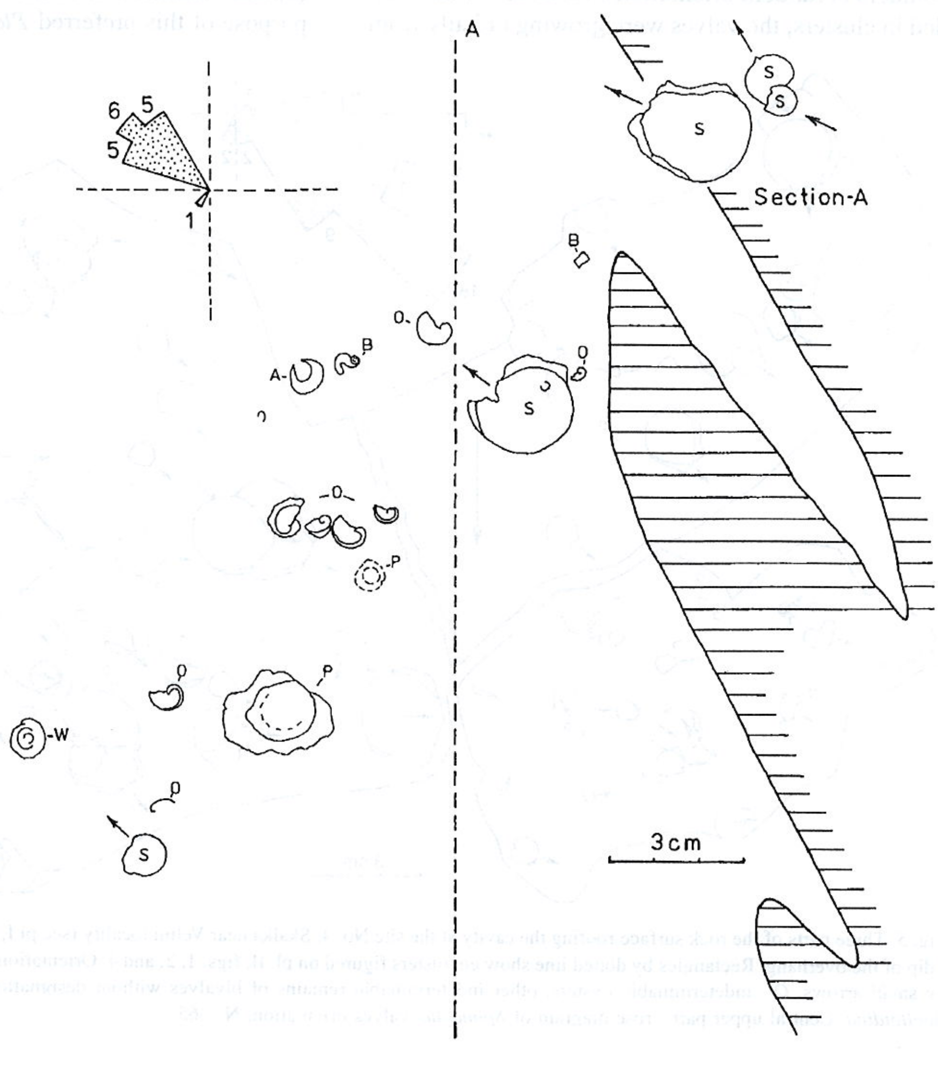

Fig. 4. Fauna encrusting rock surface at the site No. 4, close to the surface figured in text-fig. 3. P - pycnodonte oyster, W - worm, for other symbols see legend to text-fig. 3. Upper left - rose diagram of *Spondylus* orientations figured in text. figs. 3 and 4. N = 17. Note the absence of *Atreta* and *Bdelloidina* from overhangs

Search for orientation causes

1. History

Schmid (1949) summarized older data by Dacqué (1921) and Voigt (1929), who related the parallel orientations of cemented epibionts to the currents carrying food. When describing the preferred orientations of *Ostrea vesicularis* Lamarck and *Dimyodon nilssoni* (Hagenow) (in addition to the brachiopod *Crania parisiensis* Defrance) on the dead echinoid tests from the lower Maastrichtian of Hemmoor, Schmid, however, rejected this idea. He found no parallel orientations of encrusters but, on the contrary, he found echinoid tests having current-independent pattern of the epibiont distribution and of the orientation on their sloping sides. This is what later Seilacher (1960) described as the slope orientation and what we found in the BCB on the rockgrounds. *Spondylus* proper was mentioned by Schmid (op. cit.) as relatively rare encruster of Hemmoor echinoids and its orientation was not specified. Solitary valves of *Spondylus labiatus* described by Surlyk - Christensen (1974) from Ivö Klak (Upper Cretaceous of Sweden), were found cemented on the steep sides of boulders in random orientations. However, if they settled in clusters, the valves were growing radially from a centre. This orientation in clusters was advantageous for specimens preventing them from the competition for space during growth.

Seilacher (1960) considered a geotropism or phototropism as a tool for encrusting epibionts to be preferentially orientated on slopes in order to attain a position which "suits them best for gathering food and for other biological functions". These preferred orientations may have been obscured by some environmental factors, if they are very intensive (e. g., particularities of a substrate or a density of populations) and if the slope is mild. Seilacher (op. cit.) gives that rheotropism may have a similar effect, too. His conclusions about slope orientations are supported by data on various organisms (bivalves, gastropods, worms, cirripeds) colonizing bioclasts or the still living hosts.

Another example of bivalves (*Placunopsis*) encrusting the skeleton of living host (in this case of an ammonite shell) is provided by Meischner (1968). He gives also the geotropism or phototropism as the main mechanisms in which the preferred orientation of *Placunopsis* is reached. Orientation of this bivalve is not, however, on oblique or vertical shell surfaces in any way influenced by currents. Nevertheless, Meischner (op. cit.) mentions the nutritional demands as the main purpose of this preferred *Placunopsis* orientation. By

Fig. 5. Three parts of the rock surface roofing the cavity at the site No. 4, Skalka near Velim locality (see pl.I, fig. 2; text-fig. 6). Strong arrow - dip of the overhang. Rectangles by dotted line show encrusters figured on pl. II, figs. 1, 2, and 4. Orientation of all *Spondylus* valves marked by small arrows. O - indeterminable oysters, other indeterminable remains of bivalves without designation. Note absence of *Atreta* and *Bdelloidina*. Central upper part - rose diagram of *Spondylus* valves orientation. N = 65

this author, the oblique orientation of *Placunopsis* on substrate corresponds well with feeding from above, the posterior feeding margin being directed upwards. The same relation of feeding structures to the upward direction (against the planktic rain) was already stated by Seilacher (1954) for encrusters generally.

In some brachiopods (craniids, thecideans) orientated on sloping or vertical surfaces with their anterior commissure pointing downwards (see Schmid 1949, Seilacher 1960, Surlyk - Christensen 1974) a protection against the sediment downfall is believed to be the main cause of this position (see Surlyk - Christensen 1974, Houša - Nekvasilová 1984, 1987). On the contrary, many various factors were responsible for the orientation of thecideans as shown by Nekvasilová - Pajaud (1969) and Pajaud (1970).

Orientations of cemented bivalves were studied also by Fürsich (1979). *Atreta* occurring on the sloping parts of Bathonian hardgrounds of France is orientated preferentially with its hinge directed upwards and subordinately to the upper left quadrant. On the other hand, the examples from planar Bathonian substrates of France and England show the chaotic orientation of *Atreta* valves. *Spondylus* cemented to the sloping hardground surface (foreshore E of Luc-sur-Mer, N of Caen, Upper Bathonian) was orientated with its hinge- line parallel to the dip, i. e. perpendicular to the prevailing *Atreta* orientation of the same substrate. Unfortunately, the actual direction of the valve umbo (i. e., to the left or right) was not mentioned. Fürsich did not discuss the causes of the preferred bivalve orientations in detail. However, when interpreting the chaotic *Atreta* orientations on the horizontal surface of Bajocian rocky sea-floor from Cloford (England), he speculates about the absence of unidirectional currents in the respective environment. Preferred orientation of encrusters is thus believed to be a function of prevailing current direction.

The apparent taxonomic incongruities within the genus *Atreta* (see e.g. Schmid 1949, Žítt - Nekvasilová 1991, and Hodges 1991) and *Spondylus* should be taken into consideration in detailed comparisons of bivalve orientations from the localities of different ages. *Atreta*, described from the Lower Cretaceous of Štramberk (Moravia) by Houša - Nekvasilová (1984), orientated on steep rock walls of fissures similarly to the thecideans mentioned above, represents also the species (or the genus) rather different from those of the Upper Cretaceous Bohemian localities. The same might be true as regards the Bathonian (see above) and Upper Cretaceous *Spondylus* representatives.

2. Discussion on the Bohemian material

Reaction of settling *Atreta* to strictly local slope of the attachment place and not to the general slope of the substrate as well as the identical slope orientations on differently directed surfaces of the same substrate (see text-fig. 1) show, that we may reject the idea on the induction of slope orientation by currents, similarly as did Schmid (1949) for *Dimyodon nilssoni*. The same holds for the majority of our *Spondylus* sp. specimens on sloping, vertical or overhanging substrates where they are orientated identically to *Atreta*. Except for the specific angle of slope, no other substrate features seem to provoke the preferred orientation of both *Atreta* and *Spondylus*. For that reason, we tentatively follow Seilacher's (1960) wide idea on the relevance of this orientation to the best feeding and other biological functions. We do not suggest the reflection of sediment downfall in these orientations, because of probable high tolerance to sedimentation (bivalves encrusting the elevated rocky bottom parts were apparently successful also during clay sedimentation in the surrounding more depressed areas). The same holds for *Atreta*, but yet emphasized by its isochronous rich encrusting of pla-

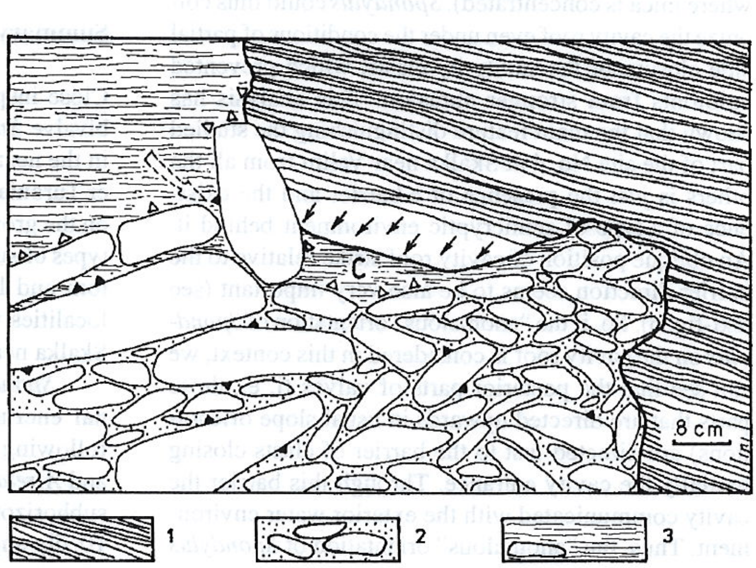

Fig. 6. The notch eroded in rock elevation and filled with sediments at site No. 4, Skalka near Velim locality. 1 - gneiss, 2 - conglomerates with lithologically varied, variously coloured matrix, 3 - overlying claystones filling also the cavity (C) and uppermost clast interstices. Black triangles on clasts - epibionts (mostly oysters and rarely *Atreta* and *Spondylus*) from the period of clast transportation and reworking. White triangles - younger phase of in situ colonization. Left arrow - direction of water penetrating the clast barrier into the cavity prior to and during clay sedimentation. Small parallel arrows - orientation of *Spondylus* sp. on the cavity roof. Note the oblique orientation of this surface strike to the barrier

nar surfaces under otherwise identical sedimentary conditions.

Looking for an explanation of "anomalous" *Spondylus* orientations (see text-fig. 5), we had to rely only upon the particularities of strictly local microenvironment. Text-fig. 6 shows a schematic reconstruction of a small cavity found at the site No. 4 of the Skalka near Velim locality, that was formed by partial filling of a rock notch by a coarse psephite and by contemporary or subsequent separation of remaining free notch space from the surroundings by large clasts. During the following sedimentation of claystones, these clasts functioned as a type of barrier. Inside the cavity roofed by the overhanging rock wall, the sediment is distinctly, even though irregularly (the barrier was only partial) impoverished in bioclasts in relation to the sediments outside the barrier. This shows the microenvironment of the cavity as substantially calmer at the beginning of clay sedimentation. *Atreta* occurring on the cavity bottom clasts shows the slope orientation demonstrating well their in situ position till the present. This bivalve could obviously live there only before the accumulating claystones covered their substrates. (*Atreta* colonized the clasts also during their preceding transportation phases but these specimens can be mostly easily distinguished from those mentioned above.) In situ encrustation by *Atreta* and *Bdellodina* has been ascertained also on the uppermost conglomerate clasts situated outside the cavity and, moreover, on clasts sheltering the mouth of the cavity.

When speculating about the timing of encrustation of the cavity roof by *Spondylus*, we noted different preservation of identically orientated valves. However, even the worse preserved ones demonstrate rather non abrasive wear (slight chemical dissolution, desquamation). Destructions of some specimens could have been also caused by falling away of small highly micaceous substrate parts (encrusted surfaces more or less coincide with foliation planes of paragneiss substrate, where mica is concentrated). *Spondylus* could thus colonize the cavity roof even under the conditions of partial side closure of the cavity by clasts, which prevented epibionts from stronger abrasion. This analysis has shown that the main feature distinguishing the studied part of the site No. 4 at Skalka near Velim from all the others is just the presence of a barrier and the existence of a type of semicryptic environment behind it. An oblique position of cavity roof strike relative to the barrier direction seems to be also very important (see text-fig. 6). So, if the "anomalous" orientation of *Spondylus* on the cavity roof is considered in this context, we can see that the posterior parts of valves (i. e., those parts that are directed upwards in usual slope orientations) are directed just to the barrier of clasts closing partially the cavity entrance. Through this barrier the cavity communicated with the exterior water environment. Thus, the "anomalous" orientation of *Spondylus* could have developed as a response to the influence of modified local hydrologic regime combined with a special position of the substrate.

The identity of orientations of all generations (at least 3) and the reached adult dimensions of some specimens confirm a relative prolongation (we suppose 10 or more years) of the whole encrustation period of the cavity. As mentioned in General notes to *Spondylus* (see above), the *Spondylus* valves found in sediments surrounding the encrusted rocks, are very fragmentary. This holds also for those found in the filling of the cavity. We suppose that these fragments, variously worn, were transported from the cavity exterior and derived from another and not just the studied part of population. In the sediments outside the cavity these fragments are yet richer. In our opinion, if *Spondylus* had inhabited the cavity during sedimentation, its not very damaged upper (left) valves would have been present in the cavity filling. As such valves are missing in this filling, we suppose that the majority of *Spondylus* specimens colonized the cavity before the beginning of clay sedimentation, when the bidirectional penetration of water through the clast barrier was not yet decreased by new sedimentary fillings and the bioclasts were possibly easily removed from the cavity. For this we suppose stronger currents, as oposed to the following period of clay sedimentation. However, even under these calmer conditions, the rocks of the sea bottom in the nearshore facies of the BCB were still abundantly colonized by *Spondylus* sp., which was possibly limited only by the advancing clay sedimentation over their substrates (see e.g., upper rock parts of the Velim site No. 4 - text-figs. 3 and 4, or the majority of other occurrences summarized in table 1). This is also true for other species of *Atreta-Bdelloidina* community.

An extraordinarily rare find of a cluster of *Spondylus* valves which show a partial radial orientation (site No. 3 at Skalka near Velim) was discussed above (see e.g. the section on different orientations).

Summary of results

Close inspection of so far known occurrences of the bivalve *Spondylus* sp. encrusting the rocky substrates in the nearshore facies of the upper Cenomanian-lower Turonian of Bohemia provided new interesting data on the growth orientation of cemented organisms. Two types of substrates were studied, namely the rocky bottom and large boulders. Geological sections at four localities were examined, the Kutná Hora-Karlov and Skalka near Velim being the most important.

Spondylus sp. formed a part of two successive faunal encrusting communities, i.e., of an oyster and following *Atreta-Bdelloidina* communities. *Spondylus* and *Atreta* were found to be chaotically orientated on subhorizontal surfaces, while on slopes of at least c. 10° dip angle they are orientated preferentially. In this case, the umbonal parts of cemented valves are directed to the upper left quadrant. *Spondylus* is rare on horizontal or subhorizontal surfaces, but both genera are frequent on the inclined ones. *Spondylus* is common also on vertical and overhanging surfaces, while *Atreta* is rare on the former and completely missing on the latter substrates. In accordance with Seilacher (1960), we designated the above mentioned type of *Spondylus* and *Atreta* orientations on more inclined substrates as the slope orientation. A detailed inspection of these bivalves' orientation has shown, however, that it was not a general slope of the substrate, but only a strictly local position of the place of settlement which raised their respective orientation response. When interpreting the causes of this preferred orientation, we tentatively consider them, in accordance with Seilacher (1960), to be a result of food-gathering needs and providing of other biological functions. On the basis of identical *Spondylus* (and *Atreta*) orientations on differently directed sloping surfaces of the same substrate (sides of boulders, walls of rock elevations) we rejected possible induction of this behaviour by currents. However, we are convinced of an urgent need for further special studies, mainly the actualistic ones, to elucidate the problem of preferred orientations in detail.

At the Skalka near Velim locality, we recently found another, rather modified types of *Spondylus* orientations. The first one is represented by a cluster of valves, which show an arrangement resembling that described by Surlyk - Christensen (1974). The valves are directed approximately radially to a centre of the cluster by their umbos and grew to the periphery, not disturbing each other.

Of greater importance is, however, a find of an encrusted rock surface where *Spondylus* settled in a rather modified slope orientation, with cemented valves directed by their hinge parts horizontally to the left or, mostly, down to the left. A colony of *Spondylus* encrusted the roof of a small cavity, which was sheltered from the surroundings by a partial clast barrier. Special interior conditions of the cavity offering a communication with the exterior environment prevailingly only through the barrier, and rather wide angle between the strike of the encrusted surface and this barrier caused probably the changed orientation of settling specimens. Under these conditions, they orientated themselves with their posterior margins to the barrier. Later on, most probably postmortally in relation to the *Spondylus* colony, the cavity was gradually filled with calcareous claystone, covering also *Atreta* specimens encrusting the cavity bottom. The same community continued, however, in encrusting the exterior rock substrates until these were completely covered by sediments of the Bílá Hora Formation.

Submitted June 30, 1994 *Translated by the authors*

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Orientace misek rodu *Spondylus*, přitmelených k pevným horninovým substrátům (Bivalvia, svrchní křída, Čechy)

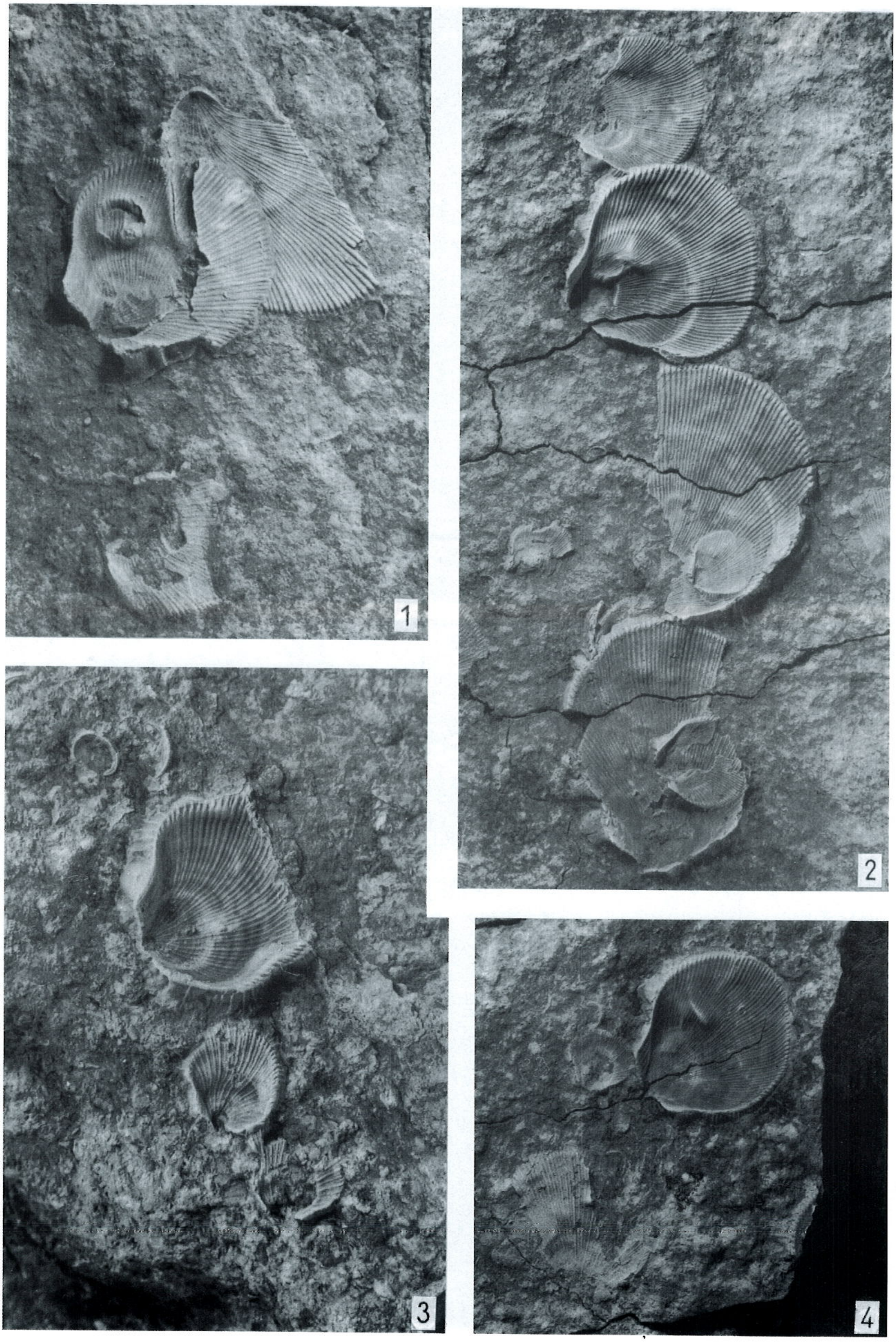
Mlži rodu *Spondylus* tvořili významnou složku společenstev, inkrustujících povrchy skalního mořského dna a balvanů v sedimentačním prostředí příbřežního vývoje českého svrchního cenomanu-spodního turonu (korycanské vrstvy, bazální část bělohorského souvrství). Na subhorizontální povrchy klastů a dna se *Spondylus* sp. přitmeloval v libovolné orientaci (chaoticky), podobně jako mlži rodu *Atreta*. Na substrátech se sklonem okolo 10° a větším však již oba rody vykazují přednostní, tzv. svahovou orientaci (slope orientation). Přitmelené misky směřují svými vrcholy do levého horního kvadrantu. Svahové orientace patrně nejlépe vyhovují požadavkům na příjem potravy a zajištění ostatních biologických funkcí (Seilacher 1960) a nejsou závislé na směru vodního proudění. Na případu osídlení převislého stropu částečně uzavřené skalní dutiny byla však z lokality Skalka u Velimi popsána přednostní orientace rodu *Spondylus*, jež je značně modifikovaná. Tato orientace byla zřejmě reakcí právě na specifický hydrologický režim dutiny.

V práci je dále popsán výskyt fragmentárního shluku jedinců se zhruba radiální orientací misek a diskutovány jsou i některé příklady přednostních orientací mlžů a brachiopodů známé z literatury. V přehledu jsou též shrnuty výskyty misek rodu *Spondylus* přitmelených k pevným horninovým substrátům, dosud zjištěné v české křídě.

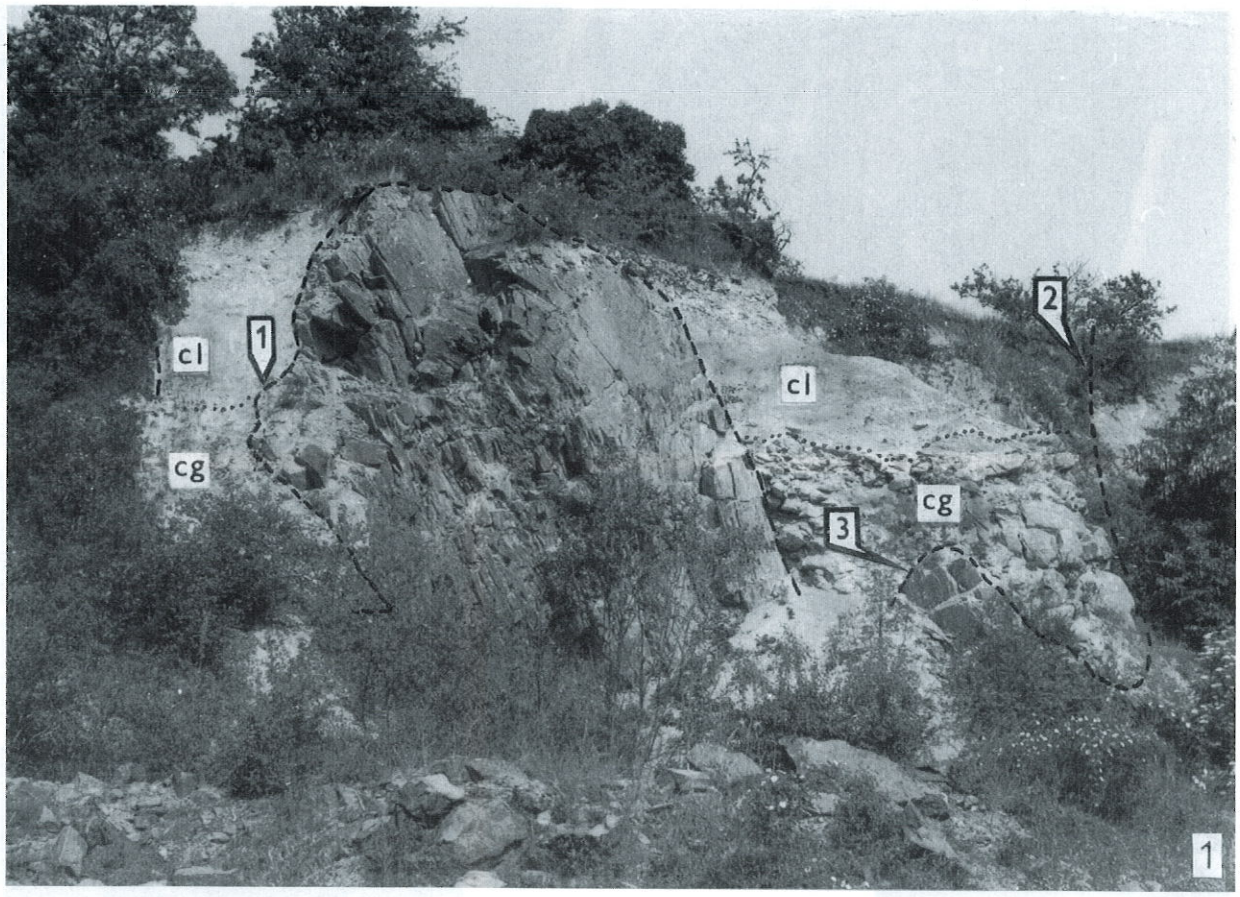
J. Žítt - O. Nekvasilová: Orientation of *Spondylus* valves cemented to the hard-rock substrates... (Pl. I)

For explanation see p. 295

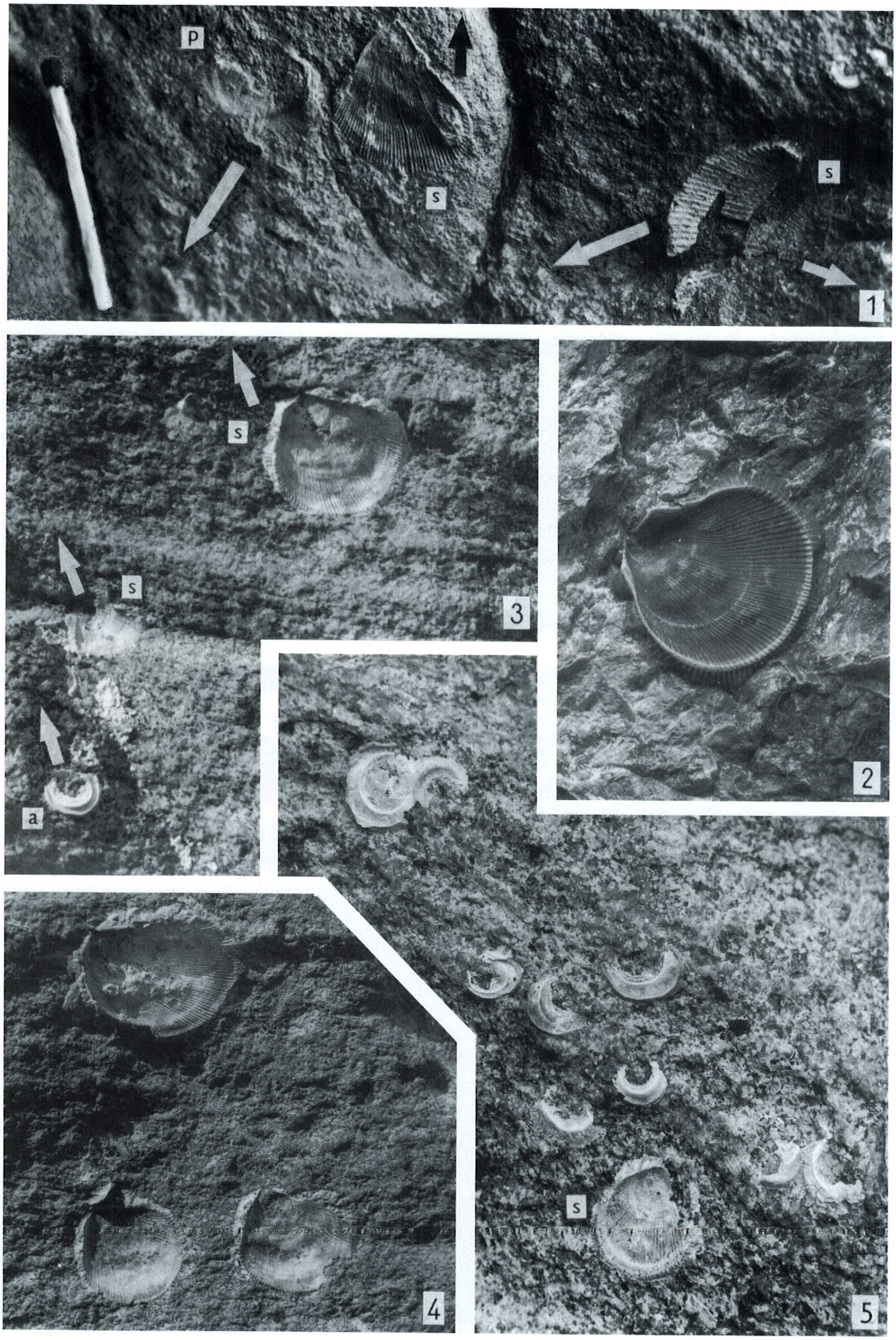
J. Žítt - O. Nekvasilová: Orientation of *Spondylus* valves cemented to the hard-rock substrates... (Pl. II)



J. Žítt - O. Nekvasilová: Orientation of *Spondylus* valves cemented to the hard-rock substrates... (Pl. III)



J. Žítt - O. Nekvasilová: Orientation of *Spondylus* valves cemented to the hard-rock substrates... (Pl. IV)



Explanation of plates

Plate I

1. Skalka near Velim, eastern part of the quarry. Depression in the rocky sea bottom filled with Cretaceous sediments, eastern view. *Dashed line* - surface of rocky bottom, *dotted* - boundary between conglomerates (cg) and claystones (cl). *c*- cavity with *Spondylus* sp. forming a part of the site No. 4.

2. Southern view of the site No. 4 at Skalka near Velim (see fig. 1 of this plate). cg - conglomerates with some clasts sheltering the mouth of the cavity (2) with *Spondylus* sp. cl - claystones filling the cavity and covering upper parts of the rock elevation with epibionts. 1 - location of surfaces figured in text-figs. 3 and 4, 2 - location of surface figured in text-fig. 5. *Photos J. Žitt, 1993*

Plate II

1-4. *Spondylus* sp. attached to the roof of the rock cavity at the site No. 4, Skalka near Velim (see pl. I, text-fig. 5). For the dip of the surfaces see text-fig. 5. 1-3.0x, 2-1.6x, 3-4.1x, 4-1.9x. *Photos J. Žitt*

Plate III

1. Skalka near Velim, western part of the quarry. Two large depressions in the rocky sea bottom. Left - depression Václav, right - depression Veronika (eastern view). cg - conglomerate, cl - claystone. 1, 2, 3 - sites Nos. 1, 2, and 3 with the occurrence of fauna encrusting the rock. Site No. 2. destroyed by quarrying. *Photo J. Žitt, 1991*

2. Detailed view of site No. 3 (see above). Orientation of attached *Spondylus* valves marked by small arrows. Large scale - 1 bar equals to 5 cm, small scales - 1 bar equals to 1cm. *Photo J. Žitt, 1986*

Plate IV

1. *Spondylus* sp. (s) and a pycnodonte oyster (p) on the rock surface at the Radim locality. The dip of substrate marked by long arrows, orientation of *Spondylus* valves by short arrows. The left *Spondylus* attached in a slope orientation, the right one in a different orientation. The length of the match is ca. 4 cm. *Field photo J. Žitt, 1988*

2. *Spondylus* sp. attached to a silicite boulder from the Líbeznice locality. Original position of substrate unknown but specimen situated as if in a slope orientation. 2.1x. *Photo J. Žitt*

3-5. Encrusters of a gneiss boulder from the Kutná Hora-Karlov locality. 3 - strongly inclined surface with *Spondylus* (s) and *Atreta* (a), both in a slope orientation (see arrows). 1.4x. 4 - *Spondylus* in a slope orientation on another part of the same substrate. 1.3x. 5 - *Spondylus* (s) and *Atreta* on a subhorizontal surface. Note chaotic orientation of valves. 1.6x. *Field photos J. Žitt, 1985*

SDĚLENÍ

Nové vydání mezinárodních zásad stratigrafické klasifikace

Subkomise pro stratigrafickou klasifikaci, která je orgánem Mezinárodní stratigrafické komise, se po roce 1976, kdy byl poprvé vydán International Stratigraphic Guide, intenzívně zabývala přípravou nového vydání. Během let 1977-1993 připravilo vedení Subkomise pod redakcí předsedy Amose Salvadora z univerzity v Austinu (USA) celkem 32 cirkulářů o celkovém objemu více než tisíce stran, které postupně rozesílalo k vyjádření jak členům Subkomise, tak předním světovým stratigrafům.

Touto sice zdlouhavou, ale cílevědomou prací se během posledních šestnácti let podařilo získat rozsáhlý a mnohdy i kontroverzní materiál, který jistým způsobem odráží "obecné mínění" v otázkách stratigrafické klasifikace, zejména v konfrontaci s prvým vydáním International Stratigraphic Guide (1976). Tento materiál byl pak použit k přípravě druhého vydání, které pod titulem International Stratigraphic Guide, a guide to stratigraphic classification, terminology, and procedure, vydaly v r. 1994 v koprodukci Mezinárodní unie geologických věd (IUGS) a Americká geologická společnost (Geological Society of America, Inc.).

Protože již prvé vydání "Guidu" zásadně ovlivnilo praktické uplatňování stratigrafických klasifikačních principů a výrazně přispělo i k jejich světové integraci (příkladem jsou i čs. zásady z r. 1978), lze s podobným vlivem počítat i u vydání druhého. Proto je účelné upozornit na některé jeho aspekty.

Třeba zdůraznit, že nové vydání nepřináší zásadní změny v klasifikačních principech a hlavních kategoriích stratigrafických jednotek (litostratigrafické, biostratigrafické a chronostratigrafické jednotky). Nově jsou však přidruženy i jednotky omezené diskordancemi (Unconformity-bounded Units) a jednotky magnetostratigrafické (Magnetostratigraphic Polarity Units). Text je v mnohém přestylizován a doplněn, což se týká např. jednotek biostratigrafických.

V obecných kapitolách o principech klasifikace, definicích, procedurách vymezování jednotek a o stratotypech je jen málo změn. Zásady potvrzují jako podmínku platnosti nově vymezovaných jednotek nutnost publikace v uznávaných vědeckých médiích, k nimž např. nepatří lokální exkurzní průvodce s omezenou cirkulací nebo abstrakty publikací či komerční tisky. Nové vydání potvrzuje omezení zásady priority (zjištěná priorita není sama o sobě důvodem ke změnám běžně užívaných názvů jednotek). V kapitole o stratotypech je zdůrazněn význam standardních definic, hraničních stratotypů a referenčních profilů (reference sections), a to i u jednotek biostratigrafických. Role typických lokalit je nezastupitelná i u těles vyvřelých hornin a v metamorfovaných souborech klasifikovaných jako stratigrafické jednotky.

K hierarchicky seřazeným litostratigrafickým jednotkám (Group, Formation, Member, Bed) je nově zařazen i Flow, tj. proud jako nejmenší definovaná část ve vulkanickém sledu. V litostratigrafické klasifikaci je potvrzena zásada užívat v názvech jednotek pouze jednoduché, v terénu aplikovatelné litologické termíny a naopak je zdůrazněna nevhodnost genetických, strukturních nebo morfologických termínů (např. žíla, diapyr, batolit).

V nově vřazené kapitole o jednotkách omezených diskordancemi je pro základní jednotku doporučen název syntem (Synthem), jehož náplň je analogická s alostratigrafickými jednotkami americ-kého stratigrafického kódu (1983). Při současném trendu sekvenční stratigrafie má však syntem jen malou naději na skutečné vžití.

Kapitola o biostratigrafických jednotkách doznala značných stylistických změn. Základním termínem zůstala biostratigrafická zóna (biozóna) s jednotlivými základními druhy (Range Zone, Interval Z., Lineage Z., Assemblage Z., Abundance Z). Vymýcen byl pojem Oppel-Zone. V názvech druhů zón byla dána přednost anglické terminologii před latinsko-řeckou, čímž se omezuje možnost překladů.

Nová kapitola o magnetostratigrafických jednotkách (Magnetostratigraphic Polarity Units) stanovuje za základní jednotku zónu polarity (Polarity Zone) s možností hierarchického dělení na subzóny a superzóny. Praxe číslování zón polarity se jistě oprávněně zamítá a odkazuje do kategorie neformálních jednotek. Rozhodně se nedoporučuje ani užívání termínů epocha, interval apod., které jsou buď příliš obecné, nebo vyhrazeny pro jiné formální stratigrafické jednotky.

Podrobně zpracovaná kapitola o chronostratigrafických jednotkách sice nepřináší základní změny v koncepcích a hlavních kategoriích, tj. stupních (Stage), odděleních = sériích (Series), útvarech (System), eratemech a eonotemech, je však místy upravená a text zpřesněn. Termín chronozóna má novou náplň a je chápán jako nehierarchická formální jednotka označující "horninová tělesa vytvořená kdekoliv na světě během doby trvání určité stratigrafické jednotky nebo geologického znaku". Tato vágní definice je zřejmě nejvýraznějším ústupkem americké praxi, která zónu chápe jako zcela obecné označení. To výrazně kontrastuje zejména s evropskou tradicí, která vždy pojímala zóny jako hierarchicky nízké jednotky především biostratigrafického obsahu.

Ve stati o sériích = odděleních (Series) se oprávněně kritizuje aplikace názvu série na litostratigrafické celky ("série" místo správného označení skupina = group se dosud i u nás ojediněle vyskytuje u autorů, kteří nejsou seznámeni se základními pravidly stratigrafické terminologie). Jména oddělení = sérií se běžně volí buď podle vztahu k útvaru (např. střední devon), nebo podle geografických názvů - v tomto případě se běžně užívají i s koncovkou -an anebo -ian (např. Chesterian Series). Snaha některých stratigrafů eliminovat u oddělení koncovku -an nebo-ian jako odlišovací znak od stupňů (např. v siluru) je proto ilegální a nemá oporu v žádném mezinárodním usnesení o stratigrafické klasifikaci.

Zvláštní pozornost se věnuje dělení prekambria, v němž jsou jako obecné chronostratigrafické jednotky uznány pouze archaikum (Archean) a proterozoikum (Proterozoic), a to v kategorii eonotémů (eonů). Principy dělení prekambrických celků jsou jinak tytéž jako u celků fanerozoických s tím, že geochronometrické jednotky, opřené o izotopová datování, nejsou jednotkami chronostratigrafickými, u nichž je závazné vymezení podle stratotypů.

V závěrečné desáté kapitole vlastních zásad se podrobně diskutuje vztah mezi jednotlivými druhy stratigrafických jednotek, jejichž nezávislost je třeba respektovat. Zvláštní postavení mají pouze chronostratigrafické jednotky jako prostředek k dosažení vlastního cíle stratigrafie při hodnocení historie Země.

Nové vydání stratigrafických zásad obsahuje slovník stratigrafických termínů se stručnými definicemi (celkem 38 str.). Vedle běžně užívaných termínů zde najdeme i názvy užívané jen zcela ojediněle (např. aurora, geolith, holozonite), vcelku však jde o slovníček užitečný.

Text nového vydání mezinárodních stratigrafických zásad je doplněn výčtem národních stratigrafických kodexů (63 položek) a obsáhlou bibliografií prací o stratigrafické klasifikaci, terminologii a procedurách (56 str.).

Nové vydání mezinárodních zásad stratigrafické klasifikace nepřináší revoluční změny a v podstatě doplňuje vydání z r. 1976. Není proto ani důvodem pro zásadnější změny národních stratigrafických kodexů, které vycházely z vydání prvého (to je případ i našich stratigrafických zásad z r. 1978). Nové vydání však může být podnětem k jistým úpravám, revizím a doplňkům stávajících stratigrafických zásad.

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