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ECOLOGICAL SUCCESSION IN UPPER JURASSIC HARDGROUNDS FROM CENTRAL POLAND

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Analysis of ecological successions in Upper Jurassic hardgrounds at Skorków (southwestern Holy Cross Mountains), central Poland, made it possible to test the general model of ecological succession proposed by Goldring and Kaźmierczak (1974). An ecological succession is not really evident in calcarenitic hardgrounds, except when developed on pelletal limestones. This is probably due to the high rate of cementation preventing community maturation. A succession is best developed in calcilutitic hardgrounds. Two additional criteria indicative of substrate consolidation are recognized: mode of oyster attachment and bivalve boring into filled formed crypts. A change from boring to nestling is recorded in some bivalves. Influence of different hardground-microhabitats on the boring pelecypod associations is recognised.

Key words: ecological succession, hardgrounds, Upper Jurassic, early cementation.

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INTRODUCTION

The present paper is aimed to test and further refine the general model proposed by Goldring and Kaźmierczak (1974) for ecological succession in hardgrounds.

Kaźmierczak and Pszczółkowski (1968) investigated Upper Oxfordian and Lower Kimmeridgian hardgrounds southwest of the Holy Cross Mts (for geological setting see Kutek 1968), recognized fossil "communities" associated with various types of hardgrounds. Some hardgrounds from that area were also studied by Kutek and Radwański (1967) and Roniewicz and Roniewicz (1968). Ecological succession and early cementation in Lower Kimmeridgian calcareous concretions from Mt. Policzko (W Holy Cross Mts), were studied by Kaźmierczak (1974).

Numerous hardgrounds occur in various types of Upper Jurassic limestones of the southwest Holy Cross Mts. Well exposed hardgrounds appear especially common in the Skórków area (fig. 1). Twenty formed

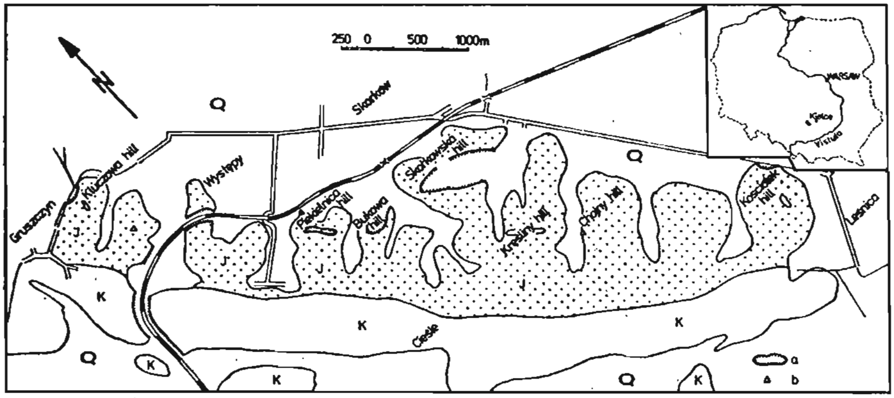

Fig. 1. Schematic map of Upper Jurassic deposits from Skorków vicinity, Kielce region. *a* large exposures *b* other outcrops; *J* — Upper Jurassic (dotted), *K* — Cretaceous, *Q* — Quaternary.

the basis for testing Goldring and Kaźmierczak's model, five of which (figs 4 and 9) served as a basis for the reconstruction of organic associations inhabiting various types of hardgrounds.

METHODS

Over 150 polished slabs cut normal to the hardground surface supplied the empirical data for the analysis of ecological succession and reconstruction of organic associations. Spatial structure of the associations was determined by the Schwerdtfeger's (1968) method (with some modifications). In every polished slab, a 2 cm thick interval including the hardground surface was divided into 2×2 cm squares, and all components of the organic associations were counted. Slabs that did not allow unequivocal recognition of the spatial structure of the association as a random, cluster, or regular one, were removed from the sample set. The last generation of borings, distribution of the encrusting organisms, and intensity of the bioturbation were studied in every polished slab using the method introduced by Palmer and Palmer (1977) for Middle Ordovician hardground.

ECOLOGICAL SUCCESSION AND LITHIFICATION

Only a single investigated hardground (fig. 2) has developed in calcirudites, namely in chalky limestones composed of lumps, pellets, onkoids, ooids, and bivalve, gastropod, and brachiopod shells forming layers or lenses in places. Most investigated hardgrounds occur in calcarenites; the latter include various oolites (wackestones, packstones, grainstones), fine-grained oolites, micro-oolites, and pelletal limestones. Finally, there are also some hardgrounds in calcilutites, represented by micritic limestones with micro-oolitic increments and shaly micritic limestones.

In order to recognize ecological succession in the hardgrounds examined, the relationship of organisms to substrate lithification (fig. 3)

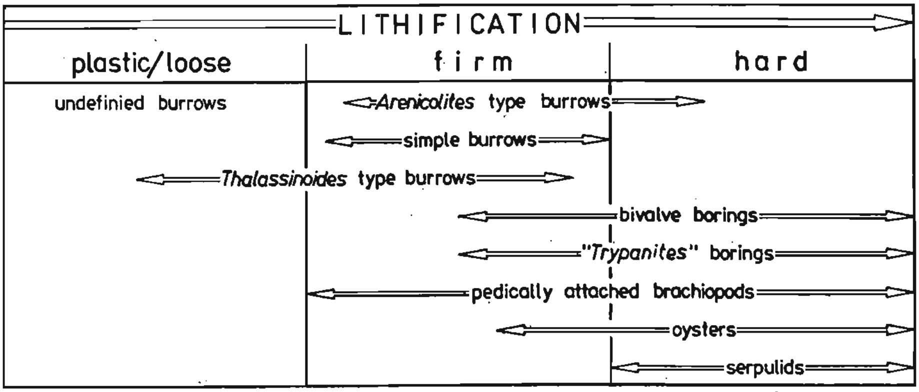

Fig. 3. Organic structures and organisms associated with three stages of substrate lithification

was studied first. Early cementation of the calcareous deposit leading ultimately to hardground formation may go either rapidly, or gradually and slowly (compare Goldring and Kaźmierczak 1974). Three successive stages of substrate consolidation can be recognized irrespective of the rate of cementation. These are: 1. plastic or loose, 2. firm, 3. hard.

In addition to the criteria given by Goldring and Kaźmierczak (1974) for recognising substrate consolidation, two other criteria are proposed in the present study: 1) boring bivalves settling burrow openings (pl. 5: 4) and bored into older borings filled with shell detritus, indicating rapid lithification of the crypt fill (pl. 5: 5 and 6); 2) the mode of oyster attachment. In the investigated hardgrounds, oysters attached to a firm substrate with as large as possible area of their shells; the near-surface crust under the shell is often fine-grained and reddish. If the substrate was hard, the oyster-shell attachment area is much smaller. Oyster shells attached to firm substrate are commonly bored by bivalves whereas those attached to hard substrates are usually not bored. This may reflect the best sites for settlement of boring bivalves in the case of firm substrates.

ORGANISMS AND ORGANIC STRUCTURES ASSOCIATED WITH THE HARDGROUNDS

Plastic or loose substrate:

(1) Undefined burrows are usually poorly expressed. They range in diameter from some millimeters to a few centimeters;

(2) *Thalassinoides*-type burrows include both the *Th. paradoxicus* (*Spongelimorpha paradoxica*) and *Th. suevicus* (*S. suevica*) morphotypes (cf. Fürsich 1973; Kennedy 1967). *Th. paradoxicus* occurs in both plastic and firm substrates, while *Th. suevicus* appears restricted to firm substrate.

Firm substrate:

(1) *Thalassinoides*-type burrows;

(2) *Arenicolites*-type burrows which include U-shaped channels ranging in diameter from 0.6 to 1.5 cm. They never penetrate deeper than 5 cm from the hardground surface. These rare trace fossils are probably to be attributed to some polychaetes;

(3) Simple burrows include three morphotypes: I — straight or slightly curved burrows (pl. 5: 1), distributed perpendicularly to the hardground surface. They range up to 2 cm in diameter and 8 cm in length; II — short, bifurcate (reverse T-shaped) (pl. 5: 2) or geniculate (L-shaped) burrows extending some 2 cm below a hardground. Their diameter is approximate 0.5 cm at openings; III — single, irregularly-shaped burrows usually with chisel-like distal ends (pl. 5: 3). They range up to 0.5 cm (opening diameter) and to 3 cm in length. Morphotype I resembles the burrows of some modern predatory crabs from the Bahamas (Shinn 1968) or *Uca* crabs (Basan and Frey 1977).

(4) Bivalve borings were produced mostly by *Lithophaga* and *Lithophaga*-like pelecypods. Other boring pelecypods occur in minor amounts. Because of the lack of body fossils extracted from the rock, the *Lithophaga*-like pelecypods cannot be identified and hence, they are refered to as form "x". Their borings are globose or bulgy in shape (their length to width ratio ranges from 0.9 to 1.1). All cross-sections of "x" and "x"-like borings are circular;

(5) "*Trypanites*" borings include three distinct morphotypes (cf. Bromely 1972): I — straight or undulating tubes ranging from 0.1 to 0.3 cm in diameter and 6—8 cm in length (= "*Trypanites*" *weisei*) (pl. 6: 3; pl. 7: 1b); II — short (at most 1 cm in length), wedge-ended (pl. 8: 3), sometimes U-shaped channels approximate 0.2 cm in diameter. Similar borings are commonly regarded as analogous to those of the modern polychaetes *Polydora* and *Potamilla* (cf. Holder and Hollman 1969); III — "*Trypanites*" borings — a group close to the first one except that the former does always show wide, globose endings (pl. 8: 2b);

(6) Pedically attached brachiopods are represented by *Zeilleria humeralis*, *Epithyris subsella*, and *Septaliphoria pinguis*;

(7) Oysters include representatives of *Nanogyra* (*N. nana*), *Exogyra*, and *Liostrea*. Their shells are commonly considerably damaged and hence, they can hardly be identified.

Hard substrate:
(1) Bivalve borings;
(2) "*Trypanites*" borings;
(3) Pedically attached brachiopods;
(4) Oysters;
(5) Serpulids include three morphotypes: *Cycloserpula* (tube forms a circle), *Tetraserpula* (tube tetragonal in cross-section), and *Dorsoserpula* (tube round with a suture).

ECOLOGICAL SUCCESSION IN CALCIRUDITIC HARDGROUNDS

Only one hardground of this type has been recorded (fig. 2: 1). It is unique in that it has formed at a layer of calcareous nodules and associated with shells of *Diceras* and *Trichites*. Close to and at those shells, there are polychaete borings represented mostly by straight or U-shaped channels. Except for some singular, U-shaped, polychaete channels approximating 1 cm in diameter, no trace fossils typical of the first stages of the ecological succession in hardgrounds (i.e. burrows) were found.

ECOLOGICAL SUCCESSION IN CALCARENITIC HARDGROUNDS

Hardgrounds occur in diverse calcarenites (grain-supported to mud-supported and coarse oolites to micro-oolites). This confirms the commonness of this hardground type claimed by Goldring and Kaźmierczak (1974).

The following succession has been recorded in coarse oolite grainstone hardgrounds (figs 2 and 4: A, B; pl. 7: 1a, 2a, 2b):

1. undefined burrows?;
2. *Arenicolites*-type burrows (figs 2 and 4: B); some generations of "*Trypanites*", *Lithophaga* and "x" borings; and encrusting *Exogyra*;
3. encrusting *Tetraserpula* (figs 2 and 4: B).

In both investigated cases, the hardground surface is flat, while depositional grains and borings together with the bivalves are truncated by erosion and corrosion (this is hardground type I of Brookfield 1974).

The following succession has been recorded in oolite wackestone hardground (fig. 2: 2).

1. undefined burrows;
2. *Lithophaga* borings and encrusting *Liostrea.*

The hardground is almost flat but there are no traces of erosion. The surface is uniformly covered with oysters and sparsely scattered *Lithophaga* borings (*Lithophaga* to *Liostrea* numerical ratio approximates 1: 4).

The following sucession has been recorded in oolite packstone hardground (fig. 2: 3; pl. 6: 3).

1. *Thalassinoides paradoxicus*;
2. *Arenicolites*-type burrows and *Lithophaga*-like borings.

There are no encrusting organisms. The hardground is a ripple surface. The ripples are symmetrical; they developed in a loose sediment and indicate an episodic wave influence upon the bottom.

Diverse ecological successions occur in hardgrounds developed in fine-grained calcarenites:

A. 1. Encrusting *Exogyra* (fig. 2—4)

The oysters occur in clusters at the flat hardground surface, while large substrate areas remain uninhabited.

B. 1. Undefined burrows;
2. A few successive boring (not biological) generations of "*Trypanites*" and *Lithophaga*-like borings (fig. 2—5).

The hardground surface is flat and covered with considerably eroded "*Trypanites*" and *Lithophaga*-like borings (pl. 7 : 1ab). The boring density ranges from 14 to 19 *Lithophaga*-like borings and from 20 to 30 "*Trypanites*" borings per 5×5 cm square (cf. Brett and Liddell 1978). This indicates high regularity and density of borings which may, however, be in part an artifact of the superposition of two distinct boring generations.

C. 1. Undefined burrows;
2. *Thalassinoides*-type burrows;
3. *Lithophaga*-like borings.

All the trace fossils show wide cementation aureoles ("halos" — pl. 3: 2) which could result from either sea-water interaction with the boring of burrow surfaces (cf. Hallam 1974, Brett and Liddell 1978), or some biochemical processes (cf. Kaźmierczak 1974).

D. 1. *Thalassinoides*-type burrows;
2. *Lithophaga* borings (fig. 2—7).

The *Thalassinoides*-type of burrows are considerably deformed by compaction. As indicated by the abrasion of the first boring generation, there was an erosional episode between the first and second boring generations (pl. 7 : 3). The borings and burrows are filled with fine-grained light-yellow sediment which may be indicative of a corrosional episode at the last stage of the hardground formation.

E. 1. Simple burrows;
2. Bivalve borings and encrusting *Exogyra*.

The ecological succession appears quite different in hardgrounds developed in pelletal limestones (figs 2 and 4:C; pl. 7 : 4a, b):

1. *Thalassinoides paradoxicus*;
2. *Thalassinoides paradoxicus*; simple burrows; first boring *Lithophaga* generation;

Table 1

Distribution of calcarenitic hardground association components in space (fig. 4: *A*). Distance below the hardground surface: *A-D*. Distance along the hardground surface: a—d. Numerals correspond to number of borings within squares.

Slab	Stage		*"Trypanites"* borings				*Lithophaga* borings			
			a	b	c	d	a	b	c	d
3	I	A	1	1	1		—	—	—	
		B	1	1	1		—	—	—	
	II	A	1	—	—		6	2	—	
	III	A	—	—	—		1	1	1	
6	I	A	—	1	—		1	—	1	
		B	2	2	—		—	—	—	
		C	1	2	—		—	—	—	
		D	1	—	—		—	—	—	
	II	A	—	1	—		—	1	—	
	III	A	—	—	—		1	2	—	
6a	I	A	5	2	1		—	1	2	
		B	2	1	—		—	—	—	
		C	—	—	—		—	—	—	
	II	A	—	—	—		—	1	—	
	III	A	—	—	—		1	2	—	
		B	—	—	—		—	1	—	
7	I	A	—	2	1	—	2	1	2	1
		B	1	1	—	1	—	1	—	1
		C	—	2	—	—	—	—	—	—
		D	—	1	—	—	—	—	—	—
	II	A	—	—	—	—	—	—	2	—
8	I	A	4	1	—		2	1	—	
		B	3	2	—		—	—	—	
	II	A	—	—	—		—	1	—	
14	I	A	1	1	—		1	1	—	
		B	2	1	—		2	—	—	
		C	1	—	—		—	—	—	
17	I	A	—	2	3	3	—	1	1	1
		B	—	—	2	4	—	—	—	—
	II	A	—	—	1	—	—	—	—	—
23	I	A	—	1	1	2	—	1	2	1
		B	—	2	3	5	—	—	—	—
		C	—		2	1	—	—	—	—
	II	A	—	—	—	—	1	—	—	—
21	I	A	1	2	2	—	1	—	1	1
		B	1	1	2	1	—	—	—	—
		C	1	2	2	1	—	—	—	—
		D	1	—	1	—	—	—	—	—
42	I	A	—	2	2	2	—	1	1	—
		B	—	1	—	1	—	—	—	—
		C	—	2	—	1	—	—	—	1

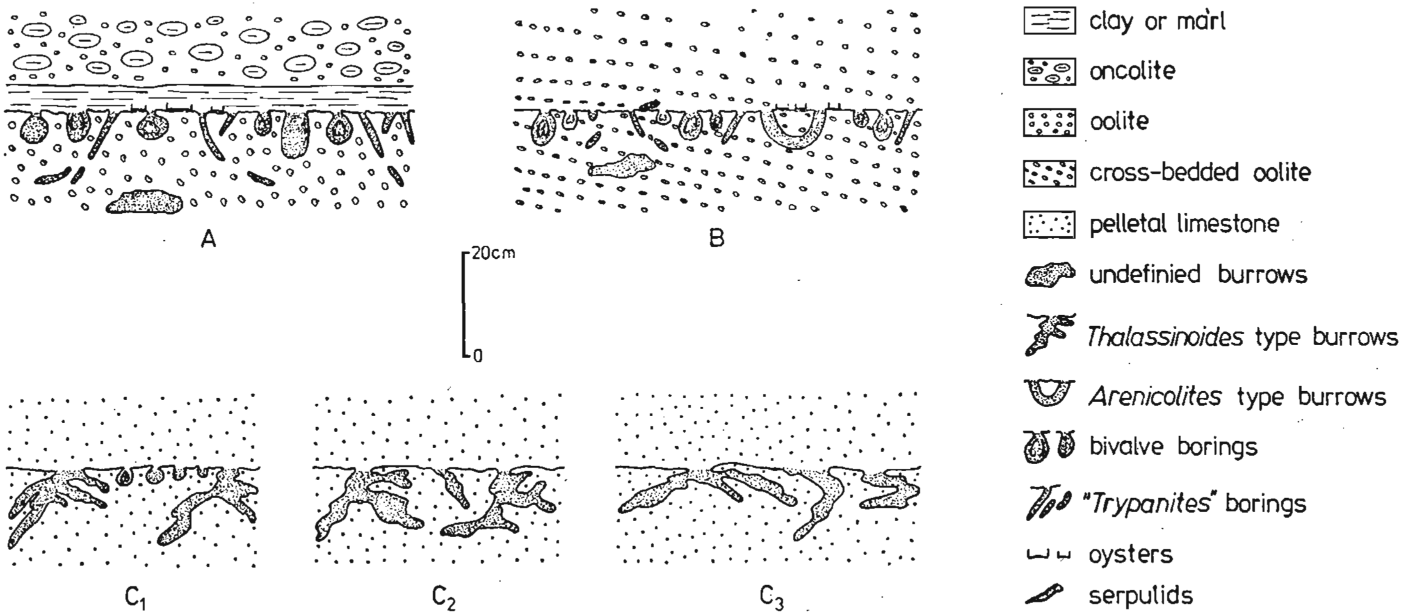

Fig. 4. Examples (A-C) of calcarenitic hardgrounds occurring in the vicinity of Skorków

3. Second boring *Lithophaga* generations and encrusting oysters (*Exogyra*).

The hardground surface is irregular due to differential erosion and corrosion of burrows and their surroundings (hardground type II of Brookfield 1974).

Except in a single case (namely, the hardground in pelletal limestones; fig. 4 : C), the first stages of ecological succession in calcarenitic hardgrounds consist of low-density organic associations, whereas the last stage associations are usually very abundant in specimens. This may indicate rapid cementation of the sediment making community maturity (typical of plastic or partly firm substrates) impossible.

The last stages of ecological succession were commonly disturbed by short-term episodes of erosion, corrosion, or sedimentation. This is indeed confirmed by the reconstruction of two hardground associations (fig. 4 : A, B).

Fig. 5. Taphonomical analysis of calcarenitic hardground association (fig. 4: A). Succession of infillings: *I* yellow fine-grained sediment (corrosion insoluble residuum); *II* brown fine-grained sediment (cemented residuum); *III* oolitic sediment. Succession of association components: *1* undefined burrows?; *2* first generation of *Lithophaga* borings (compacted crypts); *3* second (truncated crypts) and third generation of *Lithophaga* borings (infilling of crypts—*I*); *4* first and second generations of "*Trypanites*" (infilling of crypts—*II*); *5* first generation of encrusting oysters *Exogyra* (large area of shells attachment); *6* fourth, fifth and sixth generations of *Lithophaga* borings (infilling of crypts—*II*); *7* third generation of "*Trypanites*" (infilling of borings—*II*); *8* second generation of encrusting oysters *Exogyra* (shells attached to the apertures of second generation *Lithophaga* crypts); *9* seventh generation of *Lithophaga* borings (infilling of crypts—III); *10* fourth generation of "*Trypanites*" borings (infilling of borings—*III*); *11* third generation of oysters *Exogyra* (shells attached to *II* infilling of bivalve crypts or area of shells attachment is small).

Taphonomic analysis appears a necessary prerequisite for the reconstruction of the hardground associations. Three distinct developmental stages of the first hardground (fig. 4 : A) may be recognized (fig. 5) by the succession of deposits filling up the crypts and burrows. The first developmental stage of the hardground association comprises the unidentified burrows, the first to third *Lithophaga* and "x" boring (not biological) generations, the first and second "*Trypanites*" boring generations, and the first encrusting (not biological) generation of *Exogyra*. The second developmental stage comprises the fourth to sixth *Lithophaga* boring generations, the third "*Trypanites*" boring generation, and the second *Exogyra* encrusting generation. Finally, the third developmental stage comprises the seventh *Lithophaga* generation, the fourth "*Trypanites*" generation, and the third *Exogyra* generation.

Having attributed every trace or body fossil to a particular developmental stage of the hardground association, the spatial structure of the association was studied by the modified Schwerdtfeger's (1968) method; the only cluster of oysters and three slabs (of 60) with undefined burrows? were removed from the analysis. In Table 1, the results are given for 10 samples chosen at random from the sample set. The analysis shows clearly that all the components of the organic associations occur in clusters; a regularity in distribution of "*Trypanites*" borings in the slabs (slabs 3 and 21) appears as the only exception. One may also notice that the organisms of the second developmental stage of the association often settled areas uninhabited at the first stage. In turn, the organisms of the third stage almost always re-colonize areas inhabited already at earlier developmental stages of the association.

Having determined the spatial structures, the associations typical of particular developmental stages of the hardground have been reconstructed (fig. 6). It is assumed that most encrusting oysters *Exogyra* represent the first developmental stage of the association.

The second hardground (fig. 4 : B) was examined along the same lines (fig. 7), but here it was not possible to assign precisely each *Lithophaga*, "x", or "*Trypanites*" boring to a single boring generation. Colonization appears to have continuously paralleled the gradual hardening of the substrate. Changes from boring to nestling (cf. Stanley 1970) have been recognized in some *Lithophaga* specimens (pl. 6 : 1*b*). It is, however, noteworthy that even the nestlers were still able to bore the substrate, as is demonstrated by a few specimens that cut through sediment grains present within the void shells they inhabited.

Three undefined burrows, two *Arenicolites*-type burrows, a single cluster of oysters, and two specimens of *Tetraserpula* were regarded as negligible in the analysis of 45 polished slabs for recognition of the spatial structure of the hardground association (Table 2). Except for a single

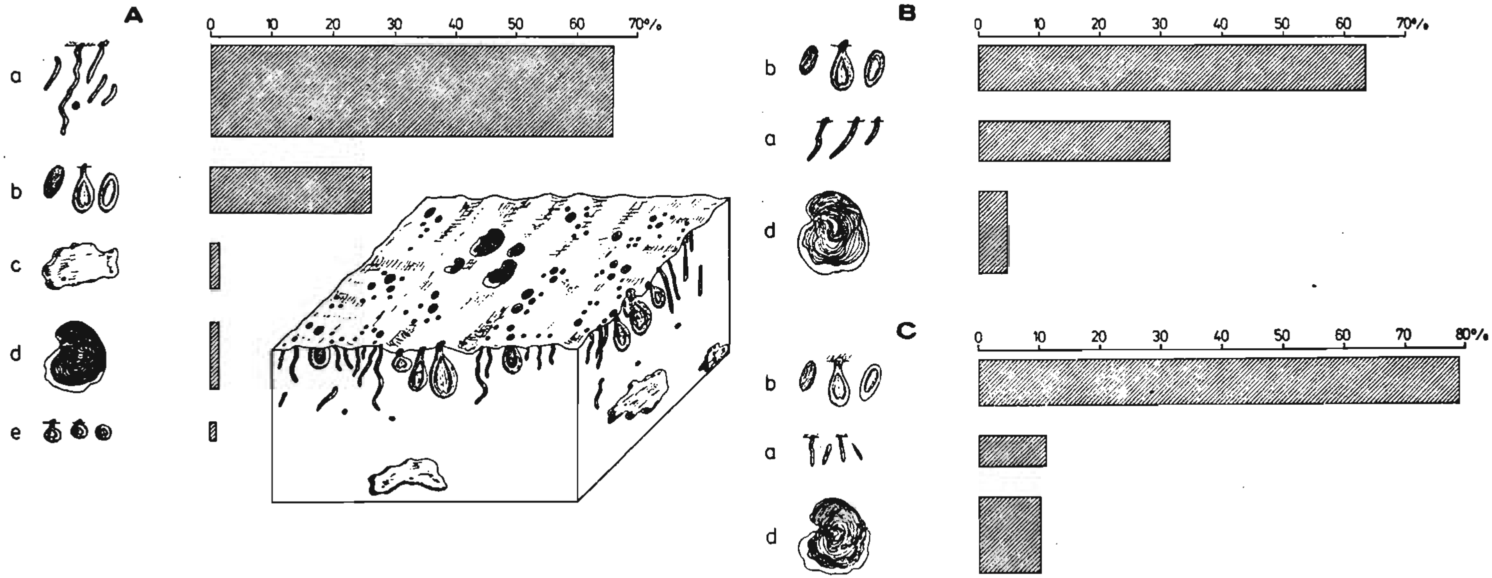

Fig. 6. Trophic nucleus and attempted reconstruction of "*Trypanites*" and *Lithophaga* associations (calcarenitic hardground — fig. 4:*A*): *A* Trophic nucleus and attempted reconstruction of "*Trypanites*" association (first stage of hardground development); *B* Trophic nucleus of *Lithophaga* association (second stage of hardground development); *C* Trophic nucleus of *Lithophaga* association (third generation of hardground development). *a* "*Trypanites*" borings, *b* *Lithophaga* borings, *c* undefined burrows?, *d* *Exogyra*, *e* "*x*" borings.

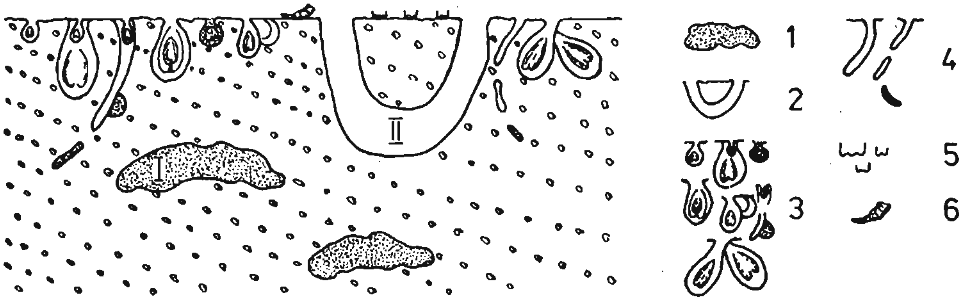

Fig. 7. Taphonomical analysis of calcarenitic hardground association (fig. 4: *B*). Succession of infillings: *I* yellow fine-grained sediment (corrosion insoluble residuum), *II* oolitic sediment.

Table 2

Distribution of calcarenitic hardground association components in space (fig. 4: *B*). Distance below the hardground surface: *A-D*. Distance along the hardground surface: a—g. Numerals correspond to number of borings within squares.

Slab		"*Trypanites*" borings							*Lithophaga* borings						
		a	b	c	d	e	f	g	a	b	c	d	e	f	g
1	A	—	—	—	—	—	—	3	—	1	4	1	1	—	2
2	A	—	—	1	—	—	—		1	1	3	1	2	3	
	B	—	1	—	—	—	—		—	—	—	—	—	—	
3	A	—	—	—	—	—			2	—	—	—	1		
	B	4	1	—	—	—			—	—	—	—	—		
3a	A	—	—	—	—	—			2	1	3	3	—		
5	A	—	1	—	—	1	—	2	2	2	—	—	1	—	1
	B	—	—	1	1	1	—	—	—	—	—	—	—	—	—
	C	1	—	—	—	1	—	—	—	—	—	—	—	—	—
7a	A	—	—	—	—				1	1	1	1			
8a	A	—	—	1					1	—	2				
16	A	—	—	—					1	—	2				
	B	—	1	—					—	—	—				
	C	—	1	1					—	—	—				
	D	—	—	1					—	—	—				
28	A	2	1	—	—	—	—	—	—	1	—	—	1	1	—

sample (slab 2) with regularly distributed *Lithophaga* and "x" borings, all components of the organic association occur in clusters.

The association can thus be reconstructed as in figure 8.

The pattern of organic association observable in the hardground developed on pelletal limestones (fig. 4 : C) appears quite different from those presented above. The association includes well developed *Thalassinoides paradoxicus* burrows. The identity of these burrows is indicated by the same general outline of the burrow systems as well as by the equality of bioturbation intensity (proportion of total burrow area to entire area of a slab or a fragment of hardground surface). The area covered

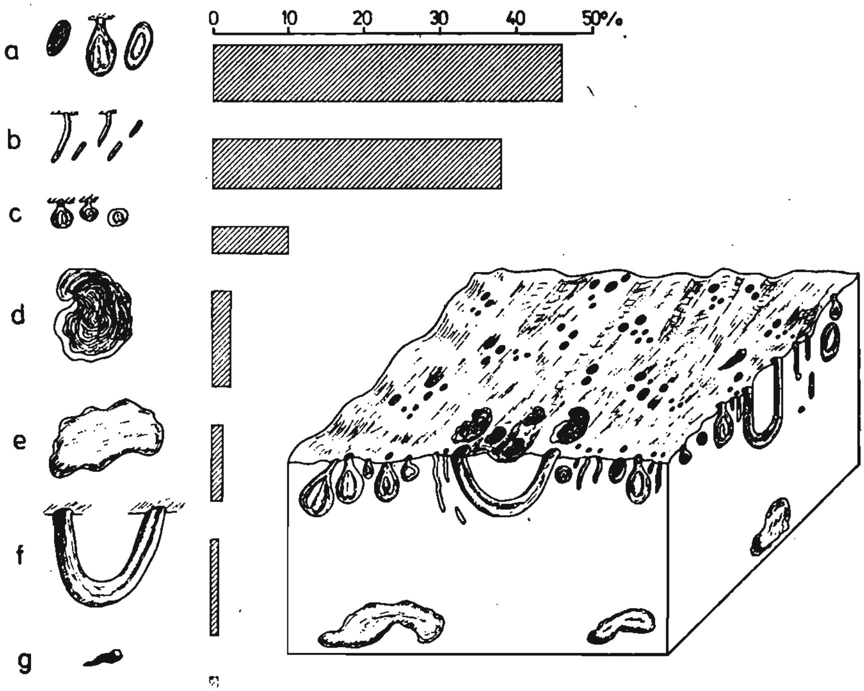

Fig. 8. Trophic nucleus and attempted reconstruction of *Lithophaga* ("x" association) (calcarenitic hardground — fig. 4: *B*). *a Lithophaga* borings, *b "Trypanites"* borings, *c* "x" borings, *d* Exogyra *e* undefined burrows?, *f Arenicolites* type burrows, *g Tetraserpula*.

with *Thalassinoides*-type burrows at and below a hardground affects considerably the possibility of settlement at the hardening substrate. In two accessible hardground-surface fragments (figs 4 : C_1, C_3), bioturbation intensities range from 28 to 46% and from 32 to 48%, respectively. In the 5 cm thick layers jut below two hardgrounds (fig. 4 : C_1, C_2), the bioturbation intensities range from 14 to 35% and from 16 to 27%, respectively.

The three hardgrounds examined formed on pelletal limestones were equally available to settlement by boring pelecypods and encrusting organisms. Nevertheless, only one (fig. 4 : C_1) has actually been colonized by two *Lithophaga* boring generations and encrusting oysters (*Exogyra*). Interestingly, the boring density is unusually constant in those areas uninhabited at earlier stages by *Thalassinoides*. In fact, boring density ranges from 7 to 13 per 5×5 cm square (it attains 21 in a single case). The encrusting oysters *Exogyra* form merely three clusters at the hardground-surface fragment (3.5 m^2).

One can hardly determine why the other hardgrounds have not been settled by any boring bivalves or encrusters. Possibly, deposition was continuous making the habitat inaccessible for both borers and encrusters (cf. Shinn 1969).

ECOLOGICAL SUCCESSION IN CALCILUTITIC HARDGROUNDS AND FIRM BOTTOMS

There are two distinct types of the ecological succession in hardgrounds and firm bottoms developed in calcilutites. One of these has been recorded in micritic limestones with micro-oolitic increments (fig. 9: D; pl. 8: 1 and 2ab). Its order is as follows:

1. Undefined burrows;
2. Trace fossils resembling modern structures considered as escape burrows of infaunal bivalves (Häntzschel 1975);
3. *Thalassinoides suevicus*; simple burrow;
4. "*Trypanites*" and bivalve borings; encrusting oysters *Exogyra*.

In shaly micritic limestones, the following succession has been recorded (fig. 9: E; pl. 8: 3):

1. *Thalassinoides paradoxicus*;
2. *Lithophaga* borings and pedically attached brachiopods *Zeilleria humeralis*, *Epithyris subsella*, and *Septaliphoria pinguis*;
4. *Lithophaga* and "*Trypanites*" borings; encrusting oysters *Exogyra* and *Nanogyra nana*.

The uniqueness of this succession consists also in the occurrence of encrusters *Nanogyra nana*, *Tetraserpula*, *Cycloserpula*, and *Dorsoserpula* at a coquinite layer covering the proper hardground. The coquina is also bored by *Lithophaga* in places.

In both types of ecological succession in calcilutitic hardgrounds, the organic associations are very rich in specimens at all developmental stages. One may therefore claim that early cementation was sufficiently slow to permit the achievement of maturity by the associations typical of all successive stages. This contrasts clearly with the development of calcarenitic-hardground associations.

In the 5 cm thick layers just below two hardgrounds showing abundant burrows of *Thalassinoides suevicus* morphotype (fig. 9: D_1, D_2), bioturbation intensities range from 9 to 15% and from 1.5 to 5%, respectively. Below the hardgrounds rich in burrows of *Th. paradoxicus* morphotype (fig. 9: E_1, E_2, E_3), to bioturbation intensities range from 14 to 26%, from 2.5 to 14%, and from 1.6 to 10%, respectively; furthermore, even the low-density systems of *Th. paradoxicus* (fig. 9: E_2,E_3) may range up to or even exceed the bioturbation intensity of some 25% close to the main arteries. One may thus conclude that bioturbation intensity is much higher in *Th. paradoxicus* than in *Th. suevicus* burrow systems. It is also noteworthy that *Th. paradoxicus* burrow systems may fill up the space either uniformly (figs 4: C and 9: E_1), or zonally (fig. 9: E_2, E_3).

Some segments of the main arteries of burrow systems developed at calcilutitic hardgrounds (those parallel to the hardground surfaces), are settled by such encrusters as *Nanogyra nana*, *Cycloserpula*, bryozoans,

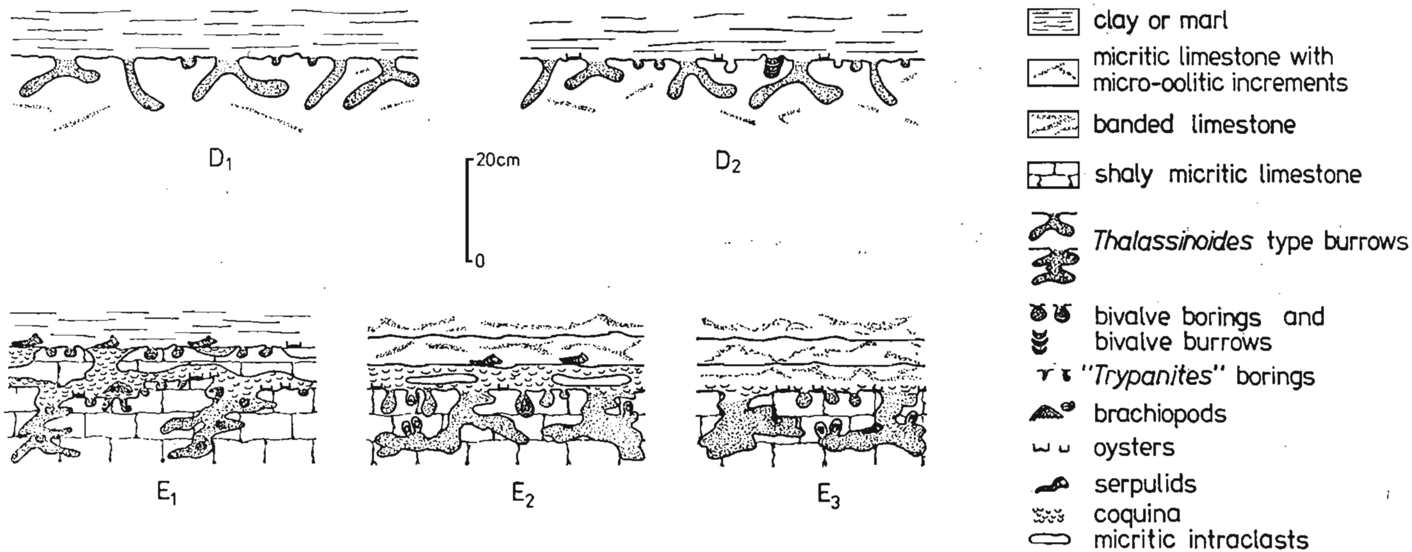

Fig. 9. Examples (*D-E*) of calcilutitic hardgrounds occurring in the vicinity of Skorków.

boring bivalves "x" and *Lithophaga* (fig. 9: E_2, E_3; pl. 8: 4ab). Just below the hardground, those segments of the burrows may form crevices (fig. 9: E_3) inhabited by the same encrusters and borers. Associations closely related in composition to those investigated in the present study have been reported from burrow systems and crevices developed in some Middle Jurassic hardgrounds (Palmer and Fürsich 1974; Fürsich and Palmer 1975); they are, however, different in their spatial structure. In the Upper Jurassic hardgrounds from Skorków encrusting bryozoans *Cycloserpula*, and *Nanogyra nana* are attached exclusively to the top surface of burrows and crevices. The boring bivalves "x" and *Lithophaga* never co-occur with the encrusters. As indicated by the taphonomic analysis (fig. 10), they settle and bore every newly formed and cemented biogenic surface. This spatial pattern of the organic association inhabiting burrows and crevices reflects probably an accumulation of food particles mostly in the top layer of water under conditions of poor circulation within a burrow system.

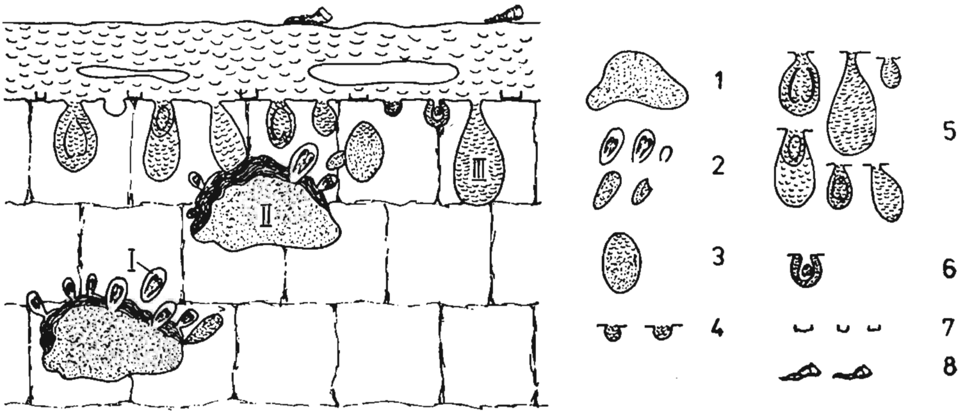

Fig. 10. Taphonomical analysis of calcilutitic hardground association (fig. 9: E_2). Succession of infillings: *I* yellow fine-grained sediment (corrosion insoluble residuum); *II* yellow to white fine-grained sediment with an admixture of shell detritus; *III* coquina; *IV* yellow fine-grained sediment (analogous to *I* infilling). Succession of association components: *1 Thalassinoides* type burrows; *2* first, second and third generations of *Lithophaga* and "x" borings (infilling of crypts — *I* and rarely *II*); *3* fourth generation of *Lithophaga* borings (infilling of crypts — *II*); *4* fifth generation of *Lithophaga* borings (infilling of truncated crypts — *III*); *5* sixth and seventh generations of *Lithophaga* borings (infilling of crypts — *III*); *6* eighth generation of *Lithophaga* borings (infilling — *IV*); *7* one (?) generation of encrusting oysters *Exogyra*; *8* one (?) generation of encrusting serpulids *Cycloserpula* and *Tetraserpula*.

Well preserved specimens of *Lithophaga* and "x" bivalves occur commonly in borings in the crevices and burrow segments. There are also the bivalve shells in borings at a calcarenitic hardground (fig. 4: B). Hence, the author was able to compare the survivorship curves (fig. 11) of two short-term associations of *Lithophaga* inhabiting different hardground-microhabitats (the sample size for "x" bivalves is inadequate to permit construction of reliable survivorship curves). In both cases, the short-term

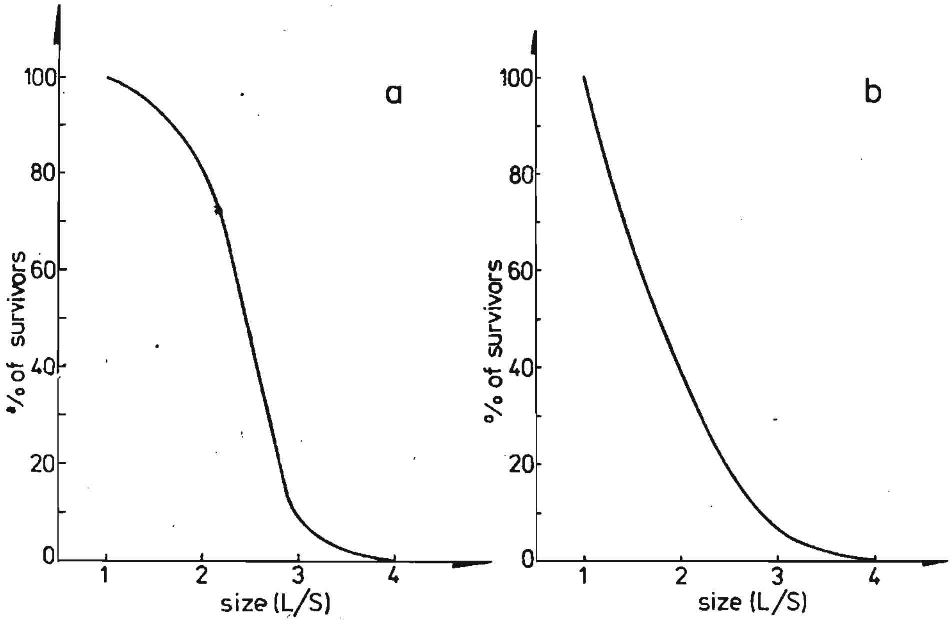

Fig. 11. Survivorship curves of *Lithophaga* associations: *a* for 148 specimens of three generations of the *Lithophaga* associated with hardground surface; *b* for 122 specimens of three generations of the *Lithophaga* associated with crevices and top of burrows system galleries parallel to hardground surface.

associations comprise three boring (not biological) generations and represent what is commonly regarded in paleoecology as populations.

The survivorship curve is convex for the *Lithophaga* association related to the hardground surface (fig. 11*a*). This shows that the juvenile mortality was low and increasing with age. In contrast, the survivorship curve is slightly concave for the other *Lithophaga* association (fig. 11*b*), indicating that the highest mortality (over 60%) affected the juveniles.

The difference in mortality patterns is probably to be explained by a difference in environmental conditions. Salinity, temperature, and space availability can be expected to be at similar levels at the hardground surface and within the crevices and burrows. Water circulation was, however, certainly much poorer in the latter biotope, resulting in lower food and oxygen supplies as well as in deterioration of the habitat by accumulating metabolites. One may then claim that the poor water circulation appears as the main (even though indirect) cause of the high juvenile mortality of *Lithophaga* in the crevices and burrow systems.

CONCLUSIONS

The present study allows a refinement of the general model proposed by Goldring and Kaźmierczak (1974) for the ecological succession in hardgrounds developed in calcirudites, calcarenites, and calcilutites.

The only investigated calciruditic-hardground succession appears entirely consistent with the model. The early successional stage is poorly developed relative to the latter stages.

The model succession for calcarenitic hardgrounds appears inadequate except for the hardground developed in pelletal limestones. In fact, the associations corresponding to particular developmental stages of the hardground in pelletal limestones largely differ in their densities. Associations equivalent to particular successional stages in other calcarenitic hardgrounds cannot be clearly recognized. Nevertheless, the associations representing the last successional stages are always well developed and comprise both borers and encrusters.

The investigated calcilutitic-hardground successions agree well with the general model. The associations related to particular successional stages are more or less constant in density. Interestingly, identical associations may arise independently under conditions of two distinct hardground-microhabitats; the same borers and encrusters inhabit a hardground surface and the top surface of crevices or burrows. Skeletal hardground (*sensu* Ziegler and Ginsburg 1974) occur at some calcilutitic hardgrounds; the coquinoid layers are considerably bored and encrusted by organisms.

Organic associations equivalent to the first successional stage are much better developed at calcilutitic than calcarenitic hardgrounds. Nevertheless, the orders of ecological succession resemble strongly each other at the later developmental stages of both hardground types.

The present study shows also clearly that the rate of early cementation imposes considerable constraints upon an ecological succession, as claimed by the model by Goldring and Kaźmierczak (1974).

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MICHAŁ GRUSZCZYŃSKI

SUKCESJA EKOLOGICZNA W ŚRÓDFORMACYJNYCH TWARDYCH DNACH Z GÓRNEJ JURY CENTRALNEJ POLSKI

Streszczenie

W pracy zweryfikowano model sukcesji ekologicznych w śródformacyjnych twardych dnach (hardgrounds), zaproponowany przez Goldringa i Kaźmierczaka (1974). Dokonano tego na podstawie analizy sukcesji w obrębie dwudziestu najbardziej czytelnych twardych den z profilu oksfordu i kimerydu okolic Skorkowa (SW obrzeżenie mezozoiczne Gór Świętokrzyskich), która wykazała że:

1) jedyny przykład sukcesji ekologicznej występującej w kalcyrudytowych twardych dnach spełnia ogólne założenia zaproponowanego modelu;

2) model sukcesji dla kalkarenitowych twardych den zgodny jest z przebiegiem sukcesji w badanych twardych dnach, szczególnie w przypadku wapieni gruzełkowych (pl. 7; fig. 3). W innych przykładach najlepiej wyrażone są ostatnie ogniwa sukcesji, ukazujące w pełni rozwinięte asocjacje organizmów drążących i narastających (pl. 6 i 7);

3) sukcesja ekologiczna w kalcylutytowych twardych dnach w pełni potwierdza założenia modelowe (pl. 8).

Analiza sukcesji ekologicznej wzbogaciła model o szereg nowych szczegółów. Dla dwóch typów twardych den odtworzono zespoły organiczne związane z kolejnymi fazami konsolidacji osadu (fig. 6, 8). Stwierdzono labilność etologiczną małżów drążących *Lithophaga* przyczepiających się często do ścian opustoszałych wydrążeń i kawern w twardych dnach (nestling) (pl. 6; fig. 3 i 4). Porównano krótkoczasowe asocjacje *Lithophaga* zasiedlających powierzchnię twardych den z odpowiednimi asocjacjami występującymi w stropach i częściowo w ścianach nor i załomów w dnach. Porównanie krzywych przeżywania (fig. 11) takich asocjacji wydaje się wskazywać, że asocjacje z nor i kawern były kontrolowane ilością pokarmu związaną z ograniczoną cyrkulacją wody w tej strefie dna.

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EXPLANATION OF THE PLATES 5—8

Plate 5

Organisms and organic structures associated with hardgrounds from the vicinity of Skorków

1. Straight simple burrow (first group of these burrows). Micritic limestone with micro-oolitic increments — Występy (fig. 2: D_2). Scale bar — 3 cm.
2. T-branched simple burrow (second group of these burrows). Micro-oolitic limestone — Skorkowska hill (fig. 2: 8). Scale bar — 2 cm.

3. Irregular simple burrow (third group of these burrows). Pelletal limestone — Kluczowa hill (fig. 2: C_3). Scale bar — 2 cm.
4. Bivalve boring (arrow) in opening of earlier burrows and borings. Shaly micritic limestone — Skorkowska hill (fig. 2: E_1). Scale bar — 2 cm.
5. Boring bivalve (5*b* — arrow) in earlier opening of bivalve crypt (5*a*) filled with detritus (arrow). Shaly micritic limestone — Bukowa hill (fig. 2: E_2). Scale bars — 2 cm.
6. Boring bivalve (arrow) in earlier boring filler with detritic sediment. Shaly micritic limestone — Bukowa hill (fig. 2: E_2). Scale bar — 1 cm.

Plate 6

Ecological succession in calcarenitic hardgrounds from the vicinity of Skorków

1. 1st type of ecological succession (there is a full description of this succession in the text):
   1) second generation of *Lithophaga* and *Lithopaga*-like borings (1*a* — narrow arrow; 1*b* — arrow with black circle on it); first or second generation of "*Trypanites*" borings (1*a* — double arrow; 1*b* — narrow arrow).
   2) third generation of *Lithophaga* borings (1*a* — arrow with black circle on it; 1*b* — double arrow); third generation of "*Trypanites*" (1*b* — double arrow).
   3) one of the sixth or seventh generation of *Lithophaga* (1*b* — narrow arrow); third generation of encrusting *Exogyra* (1*a* — little arrow).
   Oolite-grainstone — Kościółek (fig. 2: A). Scale bar — 2 cm.
2. 2nd type of ecological succession (there is full description of this succession in the text):
   1) *Thalassinoides* type burrow (arrow with black circle on it);
   2) two generations of *Lithophaga*-like borings — 1st generation (double arrow); 2nd generation (little arrow); *Arenicolites* type burrow (narrow arrow).
   Oolitic-packstone — Chojny hill (fig. 2: 3). Scale bar — 1.
3. Nestling as life habit of *Lithophaga* boring bivalves. Small bivalve (arrow) within ealier crypt with bivalve (little arrow). Oolite-grainstone — Piekielnica hill (fig. 2: B). Scale bar — 2 cm.
4. Ecological succession (1st type):
   1 Two or three generations of *Lithophaga* borings (arrows). Oolite-grainstone — Piekielnica hill (fig. 2: B). Scale bar — 2 cm.

Plate 7

Ecological succession in calcarenitic hardgrounds from Skorków vicinity

1. Strongly truncated *Lithophaga*-like borings (arrows with black circles) and "*Trypanites*" borings (1st morphotype) (other arrows).
   Micro-oolitic limestone — Występy (fig. 2: 5). Scale bars — 2 cm.
2. Other example of ecological succession (there is a full description of this succession in the text):
   1) undefined burrows (little arrow).
   2) *Thalassinoides* type burrow (arrow with black circle on it); first generations of *Lithophaga*-like structures (compacted crypts — other arrow).
   3) other generations of *Lithophaga*-like borings (slightly compacted crypts — double arrow).

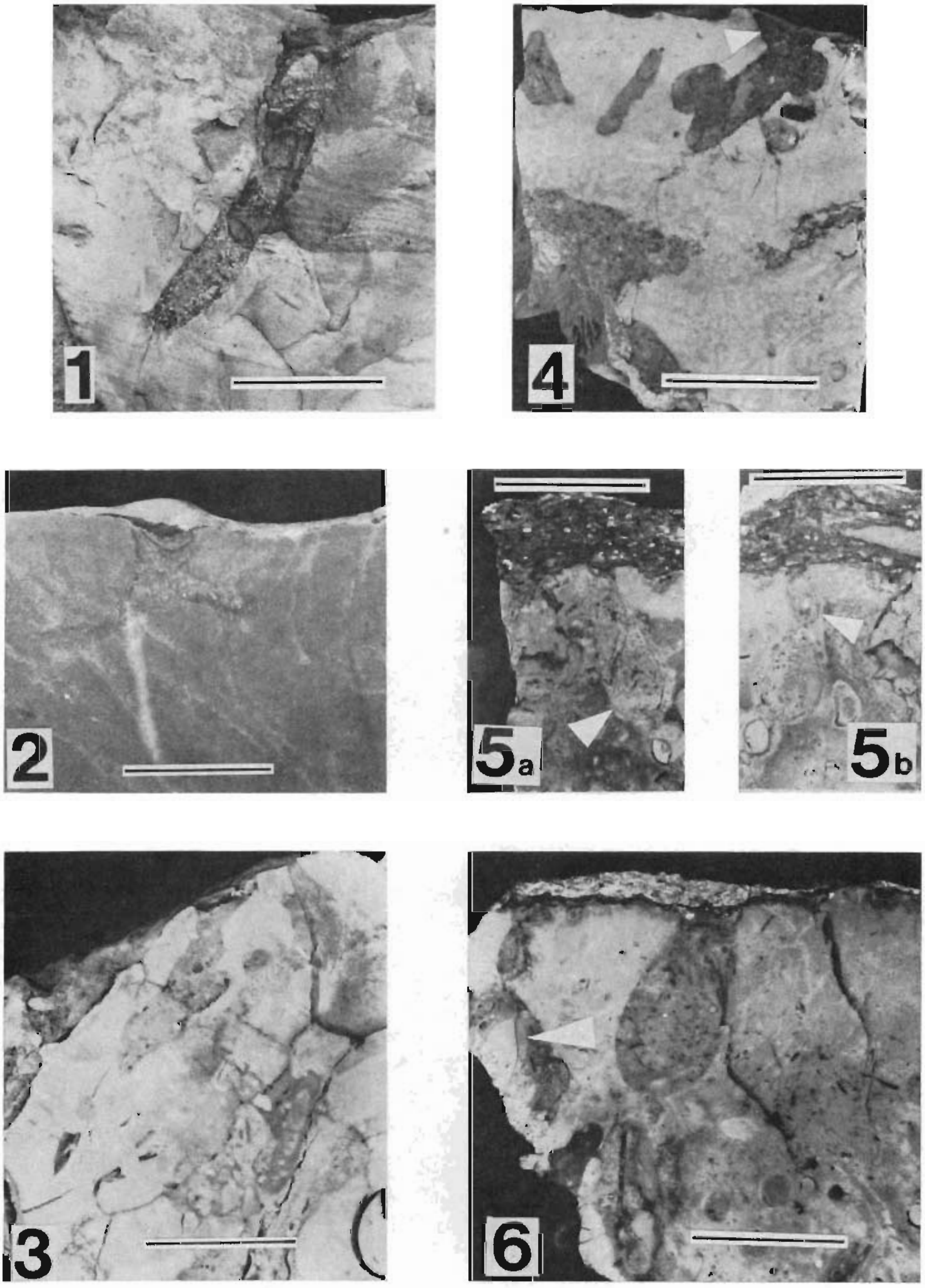
There are well visible "halos" around burrows and borings.
Micro-oolitic limestone — Kościółek (fig. 2: 6). Scale bar — 3 cm.

3. Next example of ecological succession (there is a full description of this succession in the text):
1) *Thalassinoides paradoxicus* (3*a*) type burrows (arrows).
2) a few generations of *Lithophaga*-like borings (3*b)* — individual crypts (little arrows) and bivalve borings superimposed on earlier surface trace (narrow arrow).
Pelletal limestone — Kluczowa hill (fig. 2: C_3). Scale bars: 3*a* — 2 cm, 3*b* —3 cm.
4. Next example of ecological succession:
1) *Thalassinoides* type burrow (arrow with black circle on it).
2) two (?) generations of *Lithophaga* borings — earlier generation (truncated crypts — narrow arrow); next generation (double arrow).
Micro-oolitic limestone — Bukowa hill (fig. 2: 7). Scale bar — 2 cm.

Plate 8

Ecological succession in calcilutitic hardgrounds

1. 1st type of ecological succession (there is a full description of this succession in the text):
1) undefined burrows (little arrow).
2) *Thalassinoides suevicus* type burows (arrow with black circle on it); structures similar to those of escaping bivalves (narrow arrow).
3) Strongly truncated boring (double arrow).
Micritic limestone with micro-oolitic increments (fig. 2: D_2) — Występy. Scale bar — 2 cm.
2. 1st type of ecological succession:
1) *Thalassinoides suevicus* type burrows (arrows with black circles on them) (2*a*)
2) "*Trypanites*" borings (arrows — 2*b*); bivalve borings (2*a*) — earlier crypt (narrow arrow) and in opening of this crypt new boring (litte arrow).
Micritic limestone with micro-oolitic increments — Bukowa hill (fig. 2: D_1). Scale bars — 2 cm.
3. 2nd type of ecological succession (there is a full description of this succession in the text):
1) *Thalassinoides paradoxicus* type burrows (arrows with black circles on them).
2) a few generations of bivalve borings (two are visible) — first (narrow arrow); second (litte arrow); "*Trypanites*" boring (2nd morphotype)) roof arrow).
Shaly micritic limestone — Skorkowska hill (fig. 2: E_1). Scale bar — 2 cm.
4. Main galleries of burrows system parallel to hardground surface with oncolite sheet at the top (arrows) bored by *Lithophaga*. Shaly micritic limestone — Bukowa hill (fig. 2: E_2). Scale bar — 2 cm.
5. Crevice with serpulids (arrows) mainly on the top of this crevice.
Shaly micritic limestone — Występy (fig. 2: E_3). Scale bar: 2 cm.



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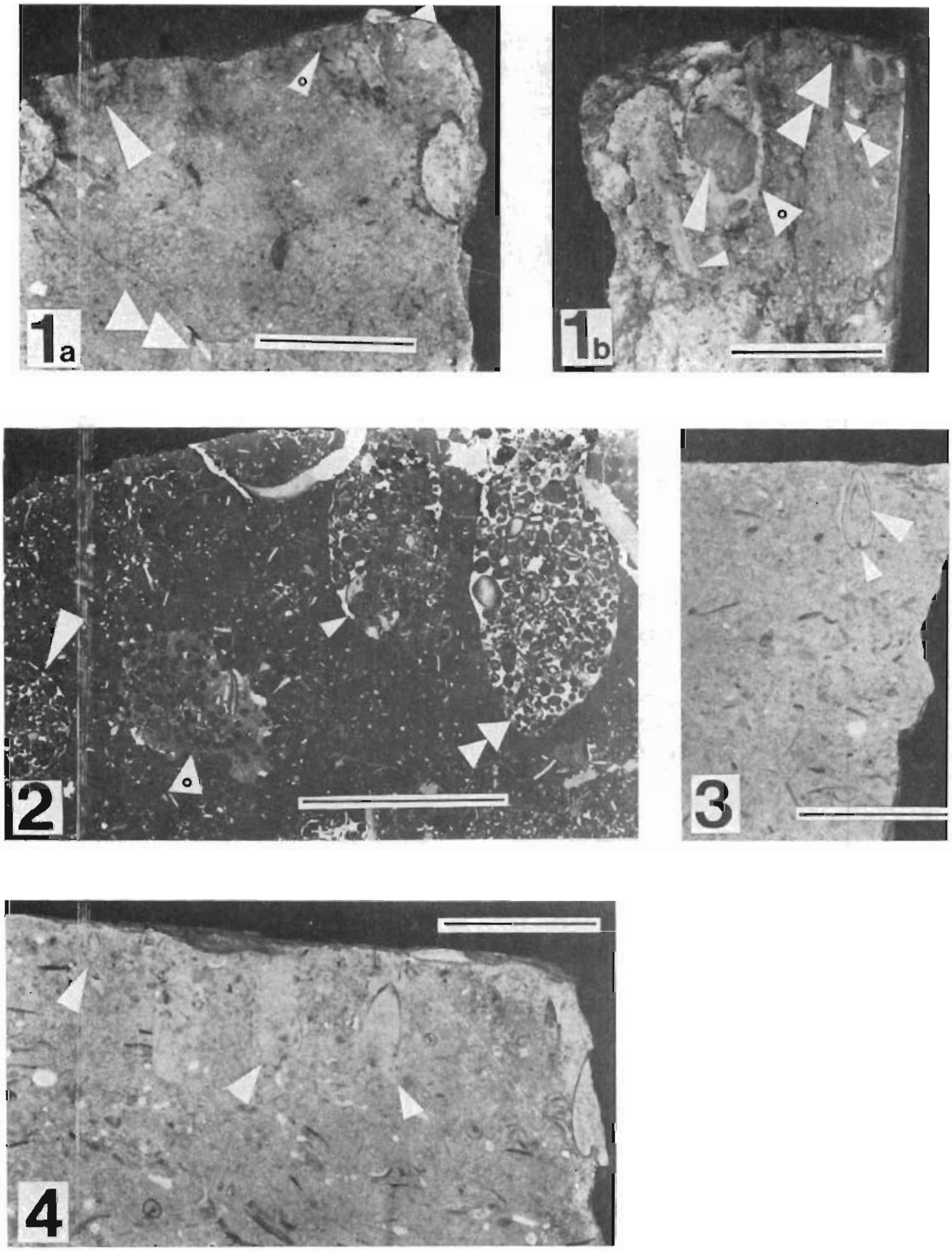

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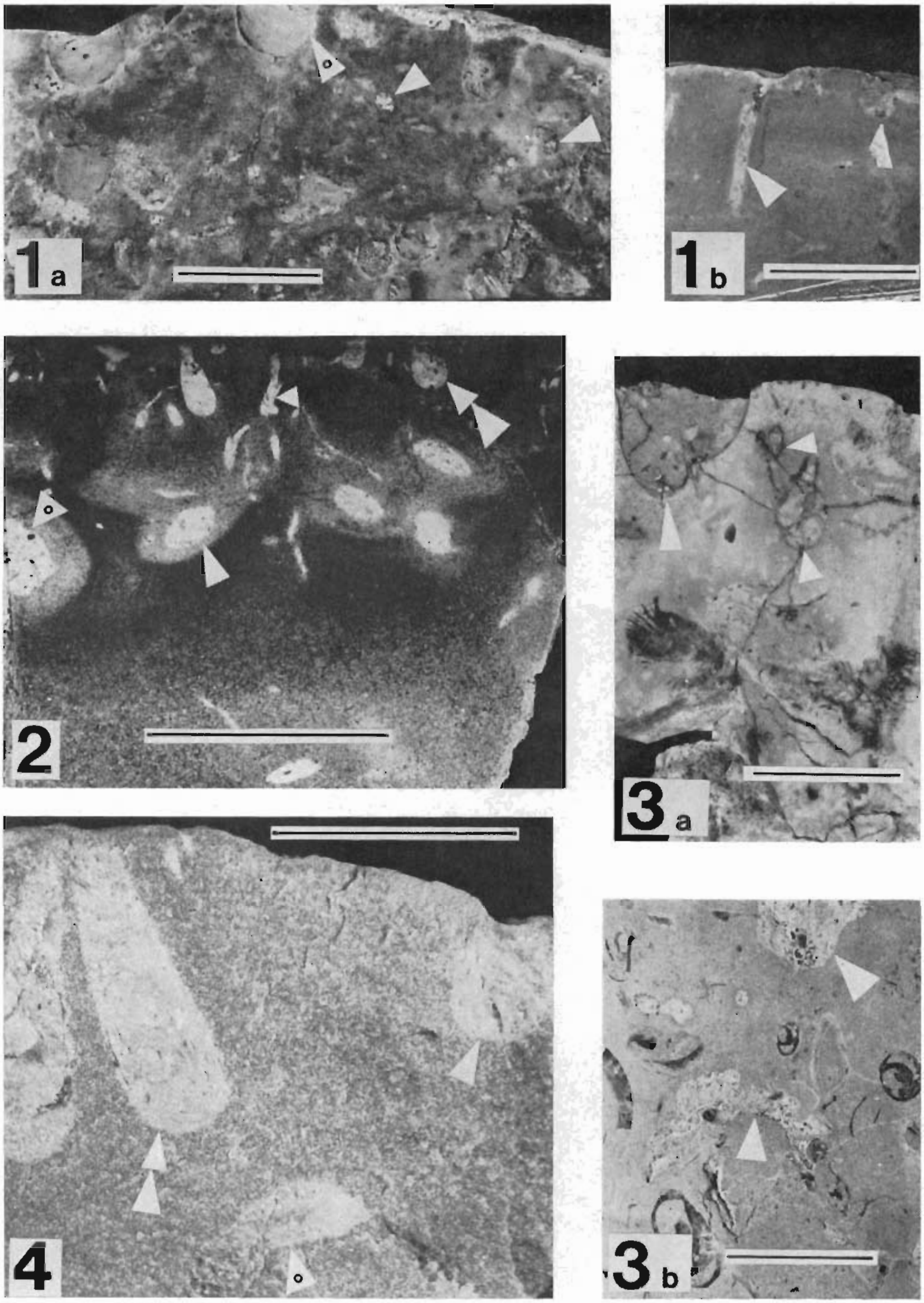

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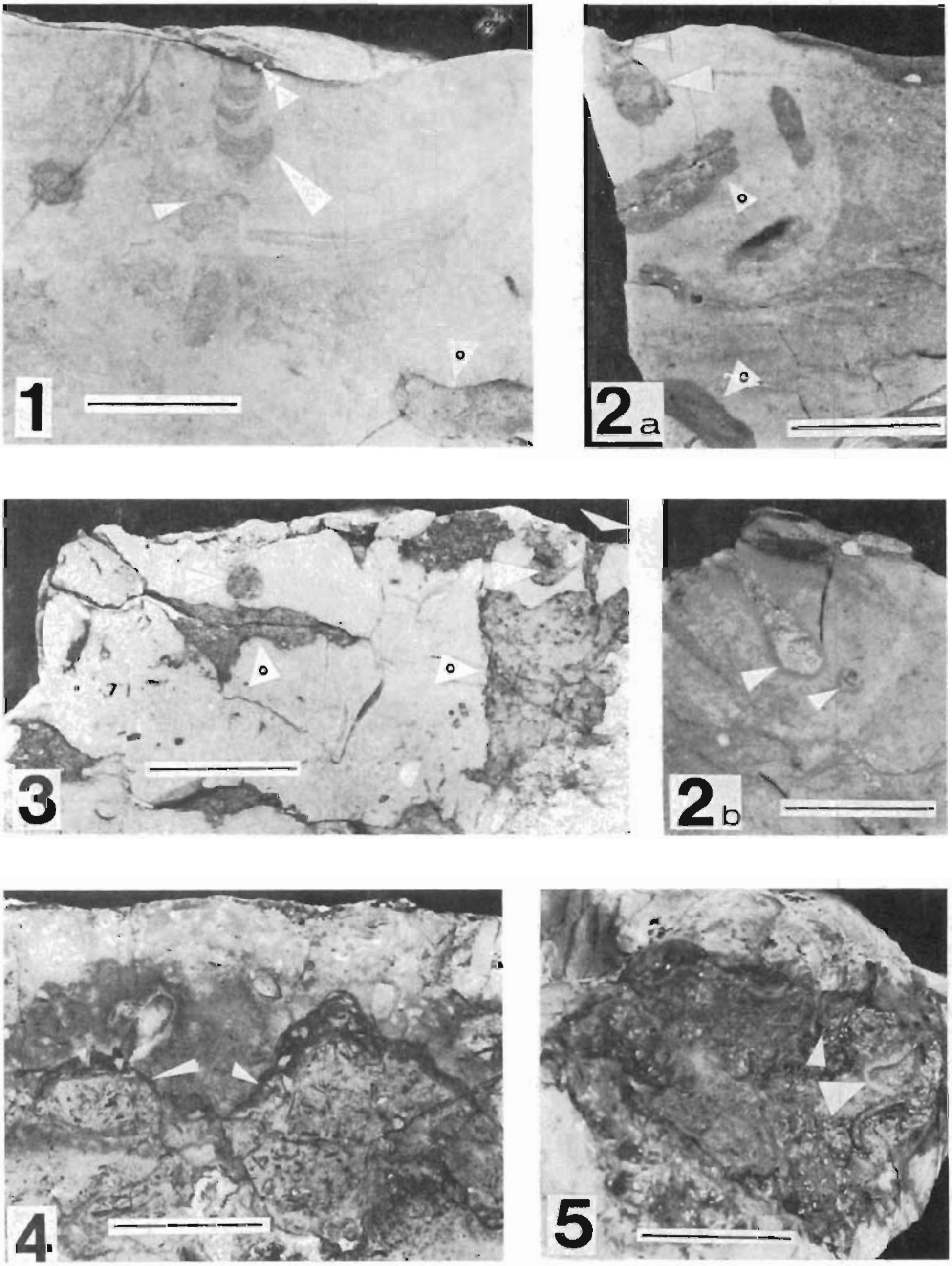

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