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HARDGROUNDS AND ECOLOGICAL SUCCESSION IN THE LIGHT OF EARLY DIAGENESIS (JURASSIC, HOLY CROSS MTS., POLAND)

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Benthic assemblages associated with Upper Jurassic hardgrounds in the Holy Cross Mts. display false, plausible, broken and real ecological succession. The breaks in the succession appear to be influenced by hydrodynamic activity, changes in salinity, pH, water chemistry, and rates of sedimentation and cementation of the carbonate deposit. The studied hardgrounds were developing in a vast shoal characterized by numerous islands and bars migrating in time and space. Environmental changes were drastic, reducing diversity of life-habitat associations to opportunistic species. Deposits were cemented by both calcite and aragonite which indicates conditions of cementation similar to those of Recent carbonate sedimentary environments.

Key words: Paleoecology, biosedimentology, ecological succession, carbonate petrology, cementation, Jurassic, central Poland.

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INTRODUCTION

VALIDITY OF THE ECOLOGICAL SUCCESSION IN PALEOECOLOGY

The theoretical concept of ecological succession, introduced by Odum (1969), concerns the development of the ecosystem. Odum wrote: "Ecological succession may be defined in terms of the following three parameters. (i) It is an orderly process of community development that is reasonably directional and, therefore, predictable. (ii) It results from modification of the physical environment by the community; that is, succession is community-controlled even though the physical environment determined the pattern, the rate of change, and often sets limits as to how far development can go. (iii) It culminates in a stabilized ecosystem in which maximum biomass (or high information content) and symbiotic function between organisms are maintained per unit of available energy flow" (*l.c.*, p. 262).

Odum (1969, Table 1) listed changes occurring in major structural and functional characteristics of developing ecosystems. He grouped 24 attributes of ecosystems under six headings: community energetics, community structure, life history, nutrient cycling, selection, pressure, and overall homeostasis. Trends which may be expected in development of ecosystems are emphasized by contrasting the situation in early and late development.

Two years later, Odum (1971) defined ecological succession again and recognized: (i) autogenic succession (succession *sensu* Odum 1969) in which community succession is biologically controlled, and (ii) allogenic succession in which community replacement is caused by physical environmental factors. The latter term (allogenic succession) has been recently criticized (eg. Wilson 1982, McCall and Tevesz 1983). I think that this term is not only a misnomer (cf. McCall and Tevesz 1983). It is a very deleterious notion which obliterates an original sense of ecological succession. Unfortunately, I have been found serious debates on allogenic succession in some paleoecological contributions (eg. Walker and Alberstadt 1975, Williams 1980, Boucot 1981). I suggest, similarly to McCall and Tevesz (1983), that a "comunity replácement" is a proper term instead of "allogenic succession".

The concept of ecological succession, of course autogenic one, has been criticized (eg. Margalef 1968, Clarke 1965) and discussed (eg. Connell and Slatyer 1977) and other models proposed.

I must realize that the concept of ecological succession is an idealized view on the certain mechanisms acting in nature. This opinion finds enough support in such observations that only small amount of ecosystems have developed in conformity with parameters of ecological succession (examples by Clarke 1965, Margalef 1968, Odum 1971, Stugren 1974, Connell and Slatyer 1977) and that the developing ecosystems usually fail to match the requirements of ecological succession, mainly because of the improbability to achieve equilibrium between biocenosis and abiotic environmental factors.

The most important look at ecological succession is presented by Connell and Slatyer (1977). They proposed three models of this mechanism, concisely described on p. 1140.

The first "facilitation" model suggests that the entry and growth of the later species is dependent upon the earlier species colonize.

A second "tolerance" model suggests that a predictable sequence is produced by the existence of species that have evolved different strategies for exploiting resources. Later species will be those able to tolerate lower level of resources than earlier ones. Thus they can invade and grow to maturity in the presence of those preceded.

A third "inhibition" model suggests that all species resist invasions of competitors. The first occupants preempt the space and will continue or inhibit later colonists until the former die or are damaged, thus realising resources. Only then can later colonists reach maturity.

This "facilitation" model is merely a short repetition of the concept of ecological succession by Odum (1969).

Paleoecologists just applied models by Connell and Slatyer (1977) to their studies (Wilson 1982, 1985, McCall and Tevesz 1983). However, traditional, since article by Johnson (1972) attitude towards ecological succession in paleoecology has still existed. Johnson (1972) assumed, partly on the basis of his observations on Recent shallow water benthic organisms, that the community is a temporal mosaic, parts of which are different levels of succession.

Papers by Halleck (1973), Kauffman (1974), Bretsky and Bretsky (1975), Walker and Alberstadt (1975), Walker and Parker (1976), Johnson (1977), Hadgorn (1978), Rollins *et al.* (1978), Harris and Martin (1979), Williams (1980) applying the concept of ecological succession to the fossil record appeared afterwards. These authors reported and discussed examples of reefoid succession, long-term succession and short-term succession (names introduced by Walker and Alberstadt 1975).

Reefoid ecosystems developing with distinctive allogenic and autogenic stages (Kauffman 1974, Walker and Alberstadt 1975, Williams 1980), and ecosystems developing within thousands and millions of years (long-term successions by Bretsky and Bretsky 1975, Walker and Alberstadt 1975, Rollins *et al.* 1979) have nothing in common with the ecological succession. Pertinent, critical opinion on above mentioned so-called reefoid and long-term successions has been found in papers by Wilson (1982) and McCall and Tevesz (1983). Since ecological succession implies ecosystem development due to biotic interactions only and during short span of time, depending on environment, from 1—10 years (McCall and Tevesz 1983) to 500—1000 years (Odum 1971), those so-called successions represent either stages of habitat colonization or community replacement.

Otherwise, examples of short-term succession require a little more attention. Scenario of the successions described by many authors is generally the same. Succession started with colonization of initial substratum (usually soft-bottom mud) by flat shells of brachiopods. These shells provided a pavement upon which either bryozoans (Harris and Martin 1979, Walker and Parker 1976) or other brachiopods (Johnson 1977) could grow. The final stages of successions included thriving either monospecific stable fauna, e.g. brachiopods (Johnson 1977) or crinoids (Harris and Martin 1979), or more diversed communities, i.e. bryozoans, gastropods, pelecypods all dominated by brachiopods (Walker and Parker 1976).

Initial substrate could be colonized by pelecypod shells, and such a pavement of shells were entirely colonized by either Ostreidae and some bryozoans and serpulids (Kauffman 1974) or crinoids (Hadgorn 1978).

None of these ancient community sequences can be accepted as undoubtful example of ecological succession. Biotic as well as abiotic factors could be accounted for such community replacement (cf. Wilson 1982, McCall and Tevesz 1983). Although one or two biocenoses (Kauffman 1974, Hadgorn 1978) could develop of their own accord, distinguishing and, even more, pointing out the biotic interactions is impossible.

Returning to Recent, even biotic interactions which should control shallow-water soft-bottom succession remain unknown (McCall and Tevesz 1983). Thus, "tolerance" and "inhibition" model by Connell and Slatyer (1977) assuming invasion and grow of later occupants due to biological interactions (depending on tolerance level of resources and on death or damage of earlier colonists, respectively) cannot be applied to the fossil record. Although Wilson (1985) claims ecological succession in Ordovician hardground fauna, the reality of such succession is remote.

Wilson (1985) reconstructed an order of community development from low-diversity pioneer assemblage through a high-diversity association to a monospecific stable fauna. Since, all species, including the late successional dominants, were present in the early stages of colonization, such succession could be classified under "tolerance" or "inhibition" model. It could be classified under models by Connell and Slatyer (1977), if it would be an example of these models. But it is very doubtful from my point of view. I have had a look at intertidal and subtidal benthic associations of Spitsbergen (Gruszczyński and Różycki in prep.) and I want to briefly regard one example.

Rocks within the intertidal zone of Spitsbergen have been colonized by algae, barnacles and gastropods forming vertical zones of dominance (fig. 1). Two species of barnacles *Balanus balanoides* and *Balanus crenatus* have coexisted within the Balanus Zone (fig. 1). *Balanus crenatus* have occupied lower part of the Zone whereas *Balanus balanoides* dominated upper part of this Zone in conjunction with *Balanus balanoides* greater dessication resistance. It is conceivable that submersion of stone fragments can result in domination of *Balanus crenatus* over *Balanus balanoides* whereby rapid burial can maintain fossil record mimicking example of "tolerance" or "inhibition" model of succession.

In the long run I drive to the main conclusion that only "facilitation" model (Connell and Slatyer 1977), i.e. concept of ecological succession by Odum (1969) can be applied with some troubles to the fossil record. General trouble is connected with the reconstruction of biotic units (cf. Lawrance 1968, Peterson 1976, see also McCall and Tevesz 1983) shortly delineated by Kauffman (1974) as such problems as: (i) nonpreservation of record, (ii) loss of record, (iii) size selection, (v) mixing, (iv) time averaging.

In order to obtain the most complete reconstruction of ancient life-habitat associations (cf. Kauffman and Scott 1976) and, at the same time, to avoid too many difficulties in taphonomic analysis (cf. Lawrance 1968) I have chosen benthic associations associated with sedimentary discontinuity sequences for study.

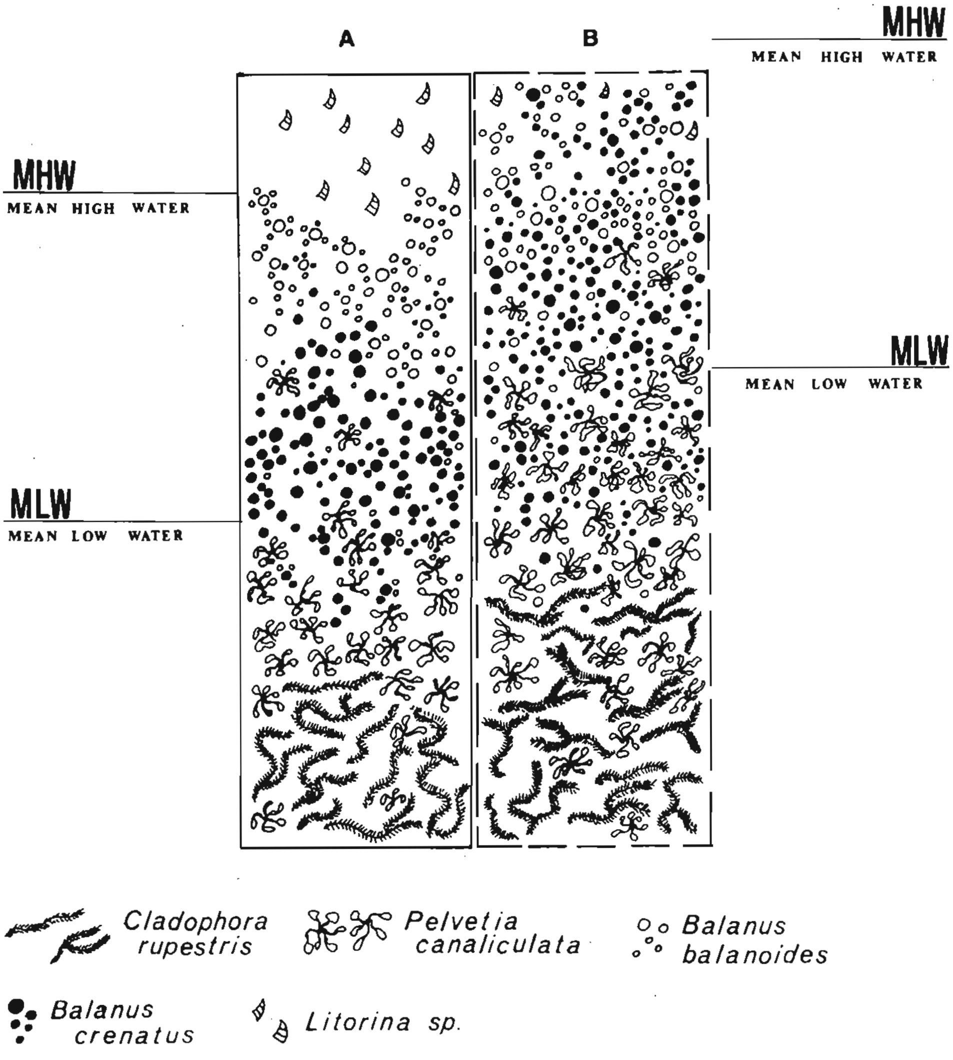

Fig. 1. *A* Zones of dominance of particular species over others within rocky shore intertidal organic association from western Spitsbergen. Coexistence of *Balanus balanoides* and *Balanus crenatus* is shown. *B* Conceivable change of mean sea level depending on unknown environmental change (e.g. configuration of the shoreline) results in dominance *Balanus crenatus* over *Balanus balanoides.*

GENERAL CHARACTERISTICS OF SEDIMENTARY DISCONTINUITY SURFACES

Sedimentary discontinuity surfaces accompanied by any organic structures have been defined as omission surfaces by Bromley (1975). They are divided (Kaźmierczak and Pszczółkowski 1968) into unlithified omission surfaces (soft bottom) and synsedimentary lithified surfaces — hardgrounds (hard bottoms). (The term hardground used to be applied in the

Polish literature to all sedimentary discontinuity surfaces accompanied by benthic associations of burrowing, boring or encrusting organisms).

Hardgrounds have been the subject of many studies: (a) classification, morphology or origin (Jaanusson 1961, Lindström 1963, Fürsich 1971, 1973, 1979, Rose 1970, Brookfield 1974, Bromley 1975, Baird and Fürsich, 1975, Fürsich and Palmer 1975, Palmer and Fürsich 1974), (b) diversity and composition of organic associations (Halleck 1973, Hölder and Hollman 1969, Koch and Strimple 1968, Goldring and Kaźmierczak 1974, Palmer and Palmer 1977, Palmer and Fürsich 1974, Brett and Liddel 1979, Palmer 1982, Wilson 1985), (c) process of hardgrounds cementation (Shinn 1969, Purser 1969, Hallam 1969, Kaźmierczak 1974, Dravies 1979, Lindström 1979, Marshall and Ashton 1980, Wilkinson *et al.* 1982).

Two or three among papers listed here have considered problem of ecological succession (Halleck 1973, Goldring and Kaźmierczak 1974, Wilson 1985).

Nevertheless the question may still be validly posed: do hardgrounds show evidence of truly ecological succession.

GENERAL AIMS OF THE STUDY

Benthic organisms are preserved in their natural position of live on hardgrounds. Trace fossils (burrows, borings, etc.) reflecting the activity or presence of organisms are also found. This evidence provides basis for considering the ecological succession of the benthic biota, i.e. the concept of ecological succession by Odum (1969) (= "facilitation" model by Connell and Slatyer 1977), of course, modified when applying to the fossil record. It is also provides a basis for testing the model of ecological succession of benthic associations in hardground formation (Goldring and Kaźmierczak 1974).

Ancient shallow marine hardgrounds, such as examined by the Author, formed in very variable environments close to sea level and therefore prone to emersion. Perhaps we should be surprised to find evidence for any ecological successions. But the cement history (diagenetic stratigraphy) may be used to test whether or not hardgrounds formed autogenically.

MATERIAL AND METHODS

Geological setting

Sedimentary discontinuity surfaces are numerous in upper Jurassic carbonate strata occurring in the SW part of the Holy Cross Mts. (see Kutek 1968) with hardgrounds displaying borings, burrows and oyster encrustation the most common type (Kaźmierczak and Pszczółkowski 1968, Kutek and Radwański 1967, Roniewicz and Roniewicz 1968, Kaźmierczak 1974, Gruszczyński 1979). This paper concerns upper Jurassic strata that crop out between Rogalów and Sobków (fig. 2) (SW Mesozoic margin of the Holy Cross Mts.). Fourteen sections displayed over fourty hardgrounds — 32 hardgrounds have been examined (fig. 3) associated with calcirudites, calcarenites and calcilulites. The strata involved can be assigned to the Sutneria platynota and Ataxioceras hypselocyclum Zones (Kimmeridgian — see fig. 3; see also Kutek 1968).

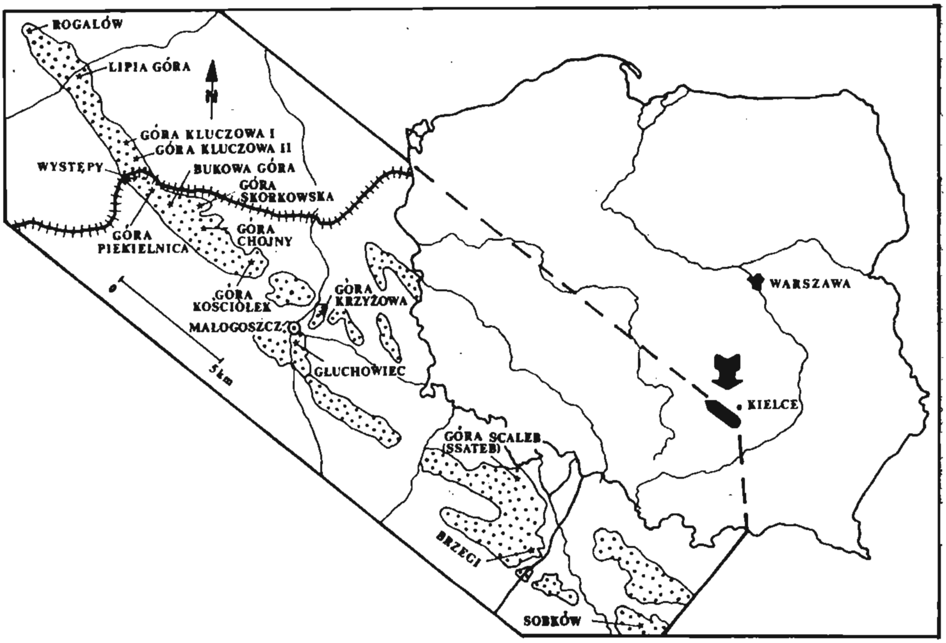

Fig. 2. Studied area is plotted on a sketch map of Poland by black polygon. Enlarged sketch of studied area shows upper Jurassic deposits (dotted) enveloped by Quaternary deposits. Main investigated exposures and quarries are marked.

Sampling and laboratory studies

Over 300 slabs were cut normal to the omission surfaces. The spatial distribution of encrusting and boring elements was evaluated using two methods: (1) by counting the elements within 10 cm squares drawn on any accessible part of a particular hardground, and (2) by counting the elements in 2 cm squares drawn on polished sections perpendicular to hardground surface (see Schwerdfeger 1969, Palmer and Palmer 1977). The activity of burrowers, here defined as intensity of bioturbation, was estimated by measuring the area on slab surfaces normal to hardground surface occupied by burrows. (Erosion depth in this case can be neglected).

About 150 artificially stained (A.R.S. + P.F.) acetate peels (Davies and Till 1968) and over 100 thin sections (in part polished and stained in accordance with recommendations of Dickson, 1965) were examined.

The fine structure of the early diagenetic cements was investigated in detail under SEM using fractured surfaces of small rock chips. These surfaces were washed with 5% solution of sodium hexametaphosphate and some were treated with 5% formic acid for a few seconds to etch out possible organic matter from mineral background. Other surfaces were polished and treated for 30 seconds in 1.5% hydrochloric acid.

RECORD OF ECOLOGICAL SUCCESSION IN HARDGROUND FORMATIONS

This section presents the evidence for the three parameters of ecological succession.

I. That community development was ordered and directional

In the model of Goldring and Kaźmierczak (1974), this parameter was presented as a succession of associations of: (1) burrowing organisms, (2) burrowing, boring, and encrusting ones and, finally (3) boring and encrusting, corresponding with three successive stages in lithification: (1) loose/plastic, (2) firm, and (3) hard. The model expressed order of appearance of biota — burrowers, then borers and finally encrusters, and direction of community development — from burrowers to encrusters.

The test of succession is the overprinting of burrows by borers and encrusters. Pair by pair procedure of testing is as follows: (1) identification of stages of substrate lithification (Appendix I); (2) recognition of biota and trace fossils associated with examined hardgrounds (Appendix II); (3) differentiation of biota and trace fossils in relation to the stages of substrate lithification (pointing out directional trend of successive colonizers); (4) delineation of order of bottom colonization from pioneer association to late successional dominants for each examined hardground.

In figure 4 (see also Appendices I and II) the biota and trace fossils associated with the hardgrounds are arranged under the three stages of lithification.

Loose bottom deposit

(1) Undefined burrows;
(2) Bivalve burrows (pl. 1: 1, 1: 2);
(3) Other bioturbation structures;
(4) U-shaped tubes;
(5) *Thalassinoides paradoxicus* (= *Spongelimorpha paradoxica*) burrows (pl. 2: 1a, c);

Firm ground

(1) *Thalassinoides paradoxicus* (= *Spongelimorpha paradoxica*) (pl. 2: 1b) and *Thalassinoides suevicus* (= *Spongelimorpha suevica*) (pl. 2: 2a, b). burrows;

(2) *Arenicolites* burrows;
(3) Single burrows — morphotype I (pl. 3: 1), morphotype II (pl. 3: 2), morphotype III (pl. 3: 3);
(4) Boring bivalves — *Lithophaga* (pl. 3: 4), *Gastrochaena* (pl. 3: 5) and "X", and *Gastrochaenolites lapidicus* (= *Lithophaga-like, Gastrochaena-like, Jouanetia*-like), and *Gastrochaenolites orbicularis* (= "X"-like) borings;
(5) *Trypanites* borings — *Trypanites weisei* (pl. 4: 1a, b, c), morphotype II (pl. 4: 2);
(6) Rare single and simple burrows — morphotype I (pl. 4: 3), morphotype II (pls. 4: 4, 5: 1), morphotype III (pl. 5: 2);
(7) *Liostrea* (pl. 5: 3a, b);

Hardgrounds

(1) *Arenicolites* burrows;
(2) Boring bivalves and bivalve borings;
(3) *Trypanites* borings;
(4) Rare single and simple borings;
(5) *Liostrea* and *Nanogyra nana* (pl. 5: 3);
(6) Traces of attachment of pedicles of brachiopods — *Zeilleria humeralis, Epithyris subsella, Septaliphoria pinguis*;
(7) *Cycloserpula* (? *Propomatoceras dentata*), *Tetraserpula* (? *Flucticularia sharpei*), *Dorsoserpula* (? *Propomatoceras keepingi*);
(8) Laminated, stromatolite-like, structures;

In figure 4 the biota and trace fossils found at each hardground locality are plotted under the appropriate order of succession. It is clear that there is not a complete ecological succession at most section. Indeed, only 15 out of 32 show this.

Where there is no evidence of pioneer occupants and late successional dominants (colonizing loose and invading hard substrate, respectively — fig. 4 — Og_5, MO_3, M_{MO_1}, M_{MO_3}, M_1), or pioneer occupants and later colonizers — invading pioneer association (colonizing loose and firm substrate, respectively — fig. 4 — FO_1), we cannot speak of succession of benthic associations but rather habitat colonizations.

Where either, there is no indication of later colonizers (invading firm substrate — e.g. Og_4, M_4) or late successional dominants (inhabitating hard substrate — e.g. Op_2, M_5) the succession again does not match the requirements of an ecological succession and may be regarded as a pseudo-succession (false succession — fig. 4). According to the introductionary assumption both habitat colonization and pseudo- (= false) succession represent associations replacement.

Where there is no record colonization typical of the first link of the order of succession, i.e. pioneer occupants invading a loose substrate, such a succession may be considered as a "secondary" succession, process starting only when the substrate was firm (fig. 4). However, disturbance allowing such a succession is indistinctive.

Gruszczyński (1979) attributed incomplete successions to high rate of cementation. This explanation is clearly insufficient in a view of many biotic and abiotic factors which could be account for such disturbances of the order of successions (see last chapter).

It must be noted, although general trend toward most diverse late successional dominants associations, enormous development of later colonizers (inhabitating firm substrate) in two cases (M_{MO_I}, V) is visible. In these cases at least two generations of *Thalassinoides suevicus* can be inferred, together with single burrows with simple structure. (Which factors are responsible for such intensity of colonizing are impossible to guess.)

Returning to the main message of this section, 13 of the locations cannot be further considered for analysis. The remaining examples do match requirements of parameter, and were subjected to test of the second parameter.

II. That the community modified the physical environment during development

Hardening, i.e. lithification of carbonate sediment is there the most important modification of habitat. The question may be posed: did this process take place because the presence and influence of organisms and the activity of organisms inhabitating the seafloor.

Lithification of carbonate sediments is related to several variants of the calcium carbonate solution-precipitation process. This is understood as filling of inter- and intra-granular space and binding grains by crystalline carbonate (cement). This is early diagenetic cement as its precipitation appears synchroneous with the colonization of the substrate as shown by relationships between cement, borings and burrows. The cement is interpreted as early diagenetic also on the basis of results of complex petrographic and geochemical analysis.

Recent carbonate cements (for reviews see Füchtbauer 1969, Bricker 1971, Bathurst 1974, 1980, Longman 1980, Milliman and Müller 1977, and others) include some which may be interpreted as formed as the result of biotic interactions (Alexandersson 1969, MacIntyre *et al.* 1971, Friedmann *et al.* 1974). The bulk of cements, including those formed within organic structures (see Alexandersson 1974), originate due to abiotic factors (see Friedmann 1975).

Thirteen types of early diagenetic cements have been recognized associated with hardgrounds. Of these only four appear to be related to organisms and organic structures (fig. 5):

(1) Bioturbation micrite, which forms irregular envelopes (= cementation aureoles) around burrows and borings, varying form a few mm to a centimeter in thickness. Thin aureoles are usually fairly stable in thickness (about 5 mm; pl. 4: 3). They are formed of micrite with a rigid, pellet-like aggregate structure but individual aggregates are so strongly cemented together as to be almost indistinguishable (pl 6: 1).

Thick (up to 2 cm or more) aureoles are only present around burrows and mainly those of *Thalassinoides paradoxicus* (pl. 6: 2a). In a single case (MO_4 — fig. 5) aureoles have been found around bivalve borings (pl. 6: 2b), but the borings appear deformed and so deep seated in relation to the hardground surface that they be considered as having formed in still loose sediment. These aureoles of bioturbation micrite on (MO_4) closely resemble those described by Hallam (1974) and Brett and Liddel (1978).

Micrite forming thick aureoles appears essentially the same as that forming thin aureoles (pl. 6: 3), differing only in the presence of opaque brown matter in centres of pellet-like aggregates or dispersed in the aureoles independently of structural pattern.

The bioturbation micrite undoubtedly originated due to the passive or active influence of burrowing and boring organisms on the sediment. The passive influence is connected with formation of circulation routes for $CaCO_3$-saturated marine water by the organisms. The flow results in precipitation of cement at the contact of a burrow with the adjacent sediment. This process is known from modern sediments (MacIntyre *et al.* 1971), but its mechanism remains unclear.

The active influence is connected with separation of organic matter by browsing organisms in the course of penetration through sediment or eating, digesting and excreting sediment and other fecal matter in or outside burrows and borings.

Under conditions of limited supply of oxygen, decay of organic matter results in the production of ammonia and, therefore, alkalization of environment (see Berner 1971, Mitterer 1971). Thus, increase of pH at the margins of burrows or borings, leads to rapid precipitation of calcium carbonate. The latter should be a calcite cement, which is connected with pollution of the micro-environment with amino acids (see Berner *et al.* 1978), but is usually a calcite and/or aragonite precipitate. This process may explain early lithification of some ancient sediments (Fürsich 1973*a*, Kaźmierczak 1974).

Organic matter present in fecal matter of crabs is considered to be the origin of thick aureoles of micrite around *Thalassinoides paradoxicus* at sites Ow, Pl_1, M_3, and M_6 (fig. 5). Such an origin is also suggested by the high content of phosphorus and carbon in the aureoles, especially at centres of micritic pellet-like aggregates.

(2) Patchy micrite is macroscopically similar to micritic bodies enveloping remains of Oxfordian sponges or Devonian stromatoporoids (Kaźmierczak and Matyja, pers. inf., 1985). There are two types of this micrite. The first is represented by irregular micrite bodies occurring among branches of *Calamophylliopsis* (pl. 6: 4) or overgrowing *Isastrea* colonies (pl. 7: 1). The second type contains irregular, patchy micritic bodies (pl. 7: 2), often unrelated to any organic (skeletal) structure but sometimes fragments of bivalve shells are embedded or adjoined to it.

The pathy micrite has most probably originated because of the activity of algae. This is shown by fimbriated relics of organic structures, embedded in the micrite. The fimbriated relics are easy to trace after staining with methyl blue and etching with 5% formic acid.

Algae living in Recent coral colonies undergo daily changes of pH (from 7.2 to 9) due to the process of photosynthesis (see Friedmann *et al.* 1974). In water saturated with Ca^{+2} and HCO^{-1} ions, and, on a smaller scale CO_3^{-2} and CO_2 these changes bring about rapid precipitation of calcium carbonate (Milliman and Müller 1977, Friedmann *et al.* 1974).

(3) Chains of pellet-like micritic aggregates (pl. 7: 4ab). It appeared impossible to find sections of such "fibres" or chains which unequivocally show that they represent tubular algae precipitating micrite in the form of pellet-like aggregates at their surfaces. However, I have found some strange structures within rigid micrite. In my opinion these are remnants of algal tubes filled up with calcite (pl. 7: 3). Studies on modern carbonate sediments implicate a genetic relationship to algae. The role of endolithic algae of the genus *Ostreobium* in initiating and accelerating the cementation process is widely known (see Schroeder 1972*a*, Kobluk 1977, Kobluk and Risk 1977*a*, *b*, Dravies 1979).

(4) Cementation aureoles — identical in structure to bioturbation micrite (pl. 7: 4a). The aureoles are developed around thin, longitudinal sparite inclusions in a micritic matrix (pl. 7: 5b). These inclusions are arranged in a network of threads or fibres in the groundmass. The nature of these inclusions remains unclear, but it should be noted that they seem similar to fragments of thread-like algae such as the Recent *Cladophora*.

Other types of early diagenetic cement present, related neither to any organism nor organic structure are:

(1) Coarse fringes 60—80 μm thick (max. 100—200 μm), built of isometric, sometimes fibrous or rhombohedral crystals generally shingle-like terminations (pl. 8: 1).

(2) Asymmetrical fringes, (a) thicker on the underside of grains and with crystal habit apparently overlapping (pl. 8: 2), (b) drop-like crystalline structures (pl. 8: 3a) or microcrystalline druses on the underside of crystals (pl. 8: 3b).

(3) Acicular/bladed fringes varying from 20 to 60 μm in thickness, with shingle- or blade-like terminations, often with needle-like inclusions (pl. 8: 4, 5, 6). Sometimes crystals represent structural extensions of the radial elements of ooids (pl. 9: 2), or completely filling ostracod carapaces (pl. 9: 1) or barely visible in some places (pl. 9: 4).

(4) Microcrystalline fringes built of closely packed rod-like crystals arranged in one (pl. 9: 3b) or two layers (pl. 9: 3c) which may be interpreted as ooid layers (pl. 9: 3a).

(5) Isometric fringes — thick (pl. 10: 1a), with irregular amoebous-like

crystals (pl. 10: 1b) with blurred, vague boundary between grains and fringes (pl. 10: 1c).

(6) Micritic and micritised fringes — formed of rigid, pellet-like micrite aggregates (pl. 10: 2).

(7) Micrite binding grains at their points of closest contact (pl. 10: 4), forming pimples and pendant structures on grain surfaces (pl. 11: 1) or completely filling intergranular spaces (pl. 11: 2). The micrite is characterized by simple — aggregational pellet-like (pl. 10: 3a, b) or rigid structure with indistinct individual aggregates (pl. 11: 3, 4). Each pellet-like aggregate is formed of isometric or, sometimes, rhombohedral crystals (pl. 11: 5a) arranged in 4—5 element units (pl. 11: 5b).

(8) Microsparite binding grains at points of closest contact as a meniscus (pl. 12: 1a, b) or filling completely intergranular pores (pl. 12: 1c).

(9) Sparite, often cut by borings (pl. 12: 2) and often (locally) replaced by chalcedony or quartz (pl. 12: 3a, b) or displays relics of silica (pl. 12: 3c).

The centres of micritic pellet-like aggregates are often spar-filled or filled with quartz. These may represent nuclei of crystallization which is proceeding around various objects, some may have been organic: there is no evidence.

In modern and ancient sediments acicular/bladed fringes are related to bioturbation structures (Ball 1967, MacIntyre *et al.* 1971, Kaźmierczak 1974), but no such correlation was found here.

Thus only hardgrounds with evidence of cements belonging to first group (i.e. cements influenced by biotic interactions) may be considered. Evidence of community modification of the substrate by lithification was found in only nine of the fifteen occurrences where the first parameter has been established (fig. 5). Of course, it is impossible to distinguish lithification connected with the living activity of pioneer colonizers — facilitating grow of later colonizers (inhabitating firm substrate) and lithification depending on later colonizers activity — facilitating invasion of late succession dominats (on hard substrate). However, such a distinction is possible at several sites. For example: M_{MO_3} (fig. 5) — indicates bioturbation micrite in conjunction with later colonizers, whereas patchy micrite at Pl_2 (fig. 5) should be attributed to pioneer colonization span of time.

Differences in the intensity of cementation caused by biota somewhat depending on colonization intensity can be a crucial point for a succession recognition.

The proportion of cements (belonging to the first group) in the seven hardground sequences is fairly large, over 20%. Intensity of bioturbation (reflecting colonization intensity) varies from 30% (fig. 5 — Pl_3) to over 50% (fig. 5 — M_3). Therefore, over 50% by volume of these sequences was occupied by, above mentioned, cements associated with traces of pioneer and later colonizers (fig. 5).

However, the proportion of these cements, in two examples (M_{MO_3}, Op_1), is low (up to 10%). In addition, the intensity of bioturbations represents at the most 20% of the hardground sequences (fig. 5).

Hence, distinction seems to be clear. The seven examples where the succession of benthic associations comply with the first two parameters are real (= autogenic) successions. The remaining examples, which comply with only the first parameter, are considered to be examples of plausible succession, which may be regarded as another kind of pseudo-succession (fig. 5), thus, another kind of association replacement.

The model proposed by Goldring and Kaźmierczak (1974) does not refer to the second parameter and so must include examples of real and pseudo-succession and is, therefore, of limited application.

III. That the community culminated as a stabilized ecosystem

In the analysis of the succession of benthic associations at hardgrounds the third parameter should refer to the great bloom of borings and encrustations, i.e. late succession dominants. These associations representing third (= last) link of the order of succession are generally characterized by higher diversity than pioneer and later colonizers associations (compare fig. 4).

Within the seven examples remaining, four (Pl_1, Ow, M_3, M_6) are remarkable because of the great number of borings and encrustations (fig. 6). For example, the section Pl_1 displays colonization by two generations of *Lithophaga* and *Gastrochaenolites lapidicus*; encrusting oysters (mainly *Nanogyra nana*), and some borings of the *Trypanites* type (morphotype II). The frequency of borings, is 7 to 13 per 0.25 cm^2 (Gruszczyński 1979). This poses the question whether or not frequency reflects maximum colonization of habitat depending on competition for space. Likewise, in Recent sediments I have found similar pattern of colonization of the fine-grained sand substrate by polychaetes (Gruszczyński and Różycki in prep.). In both cases the question remains unsolved.

This late dominants association is especially well seen at site M_3 (fig. 6), where polarization of the fauna, similar to that of middle Jurassic hardground described by Palmer and Fürsich (1974), Fürsich and Palmer (1975) is found (pl. 13). The hardground surface was inhabited by bivalve *Lithophaga*, *Gastrochaenolites lapidicus*, "X" and *Gastrochaenolites orbicularis*, and possibly polychaetes (borings of the *Trypanites weisei* and *Trypanites* — morphotype II), encrusted by oysters *Nanogyra nana*, and was a substrate for attachment of the brachiopods *Zeilleria humeralis* and *Septaliphoria pinguis* (pl. 13: 1, 2a). Networks of *Thalassinoides paradoxicus* burrows embrace more diverse encrusting fauna. Fragments of stromatolite-like structures (columnar and laminar) (pl. 13: 2b), serpulids (mainly

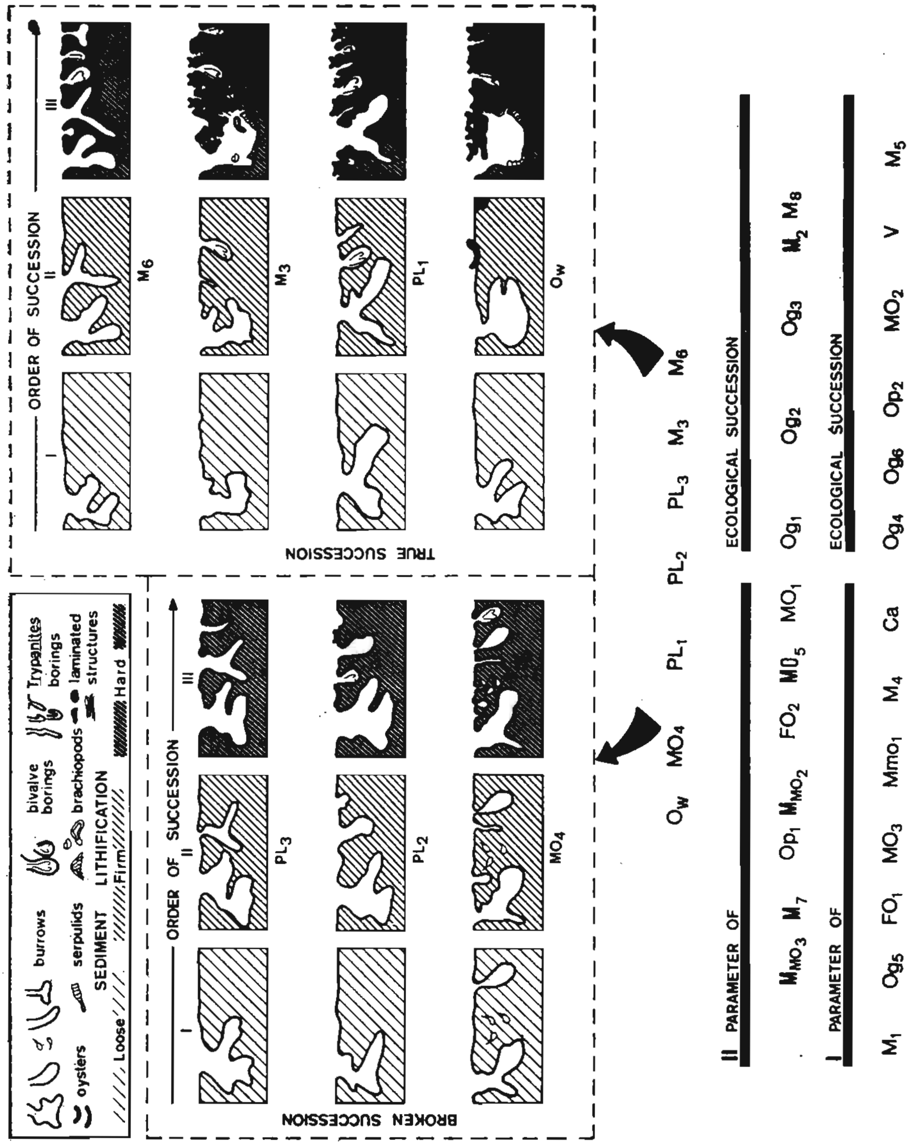

Fig. 6. The third step of ecological succession test of hardgrounds (against third parameter). Diversity of organic associations representative for successive links in conjunction with single hardgrounds is shown. Broken and true successions are distinguished.

Cycloserpula), oysters (mainly *Nanogyra nana*), and traces of attachments by the brachiopods *Zeilleria humeralis*, *Septaliphoria pinguis* and *Epithyris subsella* to walls of burrows are also found.

In order to explain the above differences an analysis of survivorship curves of two short-period *Lithophaga* associations was made (see Gruszczyński 1979). Both associations contain three generations of bivalves, re-

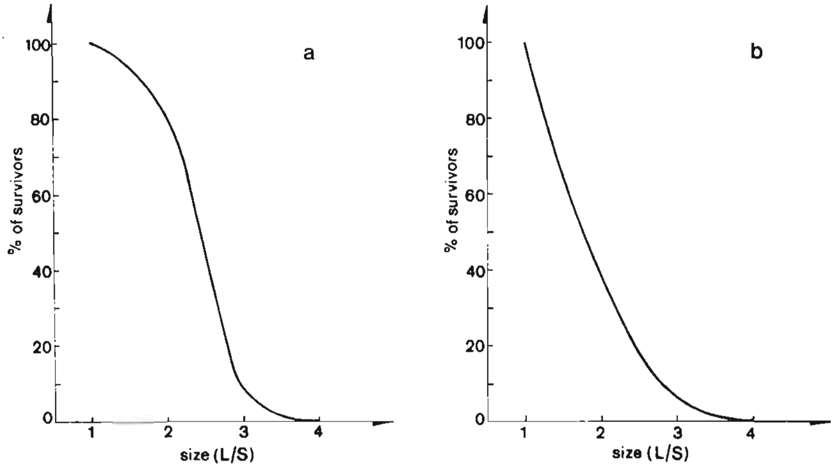

Fig. 7. Survivorship curves of *Lithophaga* associations. *a* for 148 specimens of three generations of the *Lithophaga* associated with hardground surface; *b* for 122 specimens of three generations of the *Lithophaga* associated with crevices and top of *Thalassinoides paradoxicus* burrows network parallel to hardground surface. The figure is adapted from Gruszczyński (1979).

presenting populations as usually understood in paleoecology (see Scott and West 1976). The curve is concave in the case of *Lithophaga* association related to *Thalassinoides paradoxicus* burrow networks (fig. 7), indicating maximum mortality of juvenile individuals (over 60%), and convex in the case of the association related to the hardground surface (fig. 7), suggesting increasing mortality with age of individuals. The difference may be explained by the changing activity of an abiotic factor, i.e. circulation of nutrient-supplying water since other factors (salinity, temperature, and light penetration) appear to be of secondary importance here. Increased mortality of juvenile bivalves was presumably due to low water circulation in burrows, leading to both shortage of food and temporary poisoning of environment with products of metabolism (e.g. phosphorus — see Odum 1962).

The lack of a fully developed association of boring and encrusting organisms (i.e. the last link of the order of succession) in the remaining hardground formations (MO_4, Pl_2, and Pl_3 — see fig. 6) may be explained by the high stress of abiotic environmental factors or interaction of biotic and abiotic factors, inhibiting free development of the association. So besides associations replacement and true succession we may also have examples of broken (= autogenic) succession MO_4, Pl_2, Pl_3 (fig. 6), describing ecosystems not reaching culmination point in their development.

The analysis of hardgrounds environment may help in identification of factors precluding or inhibiting development of the ecological succession (habitat colonization, plausible succession and broken succession, respectively).

HARDGROUND ENVIRONMENT

I made an attempt to reconstruct the sedimentary environment of hardgrounds beginning with a reconstruction of the history of selected sequences made with reference to (a) the initial mineralogy of early diagenetic cements, (b) the mineralogical and morphological transformation of these cements, (c) the character of sediment filling burrows and borings, and (d) the detrital grains and skeletal fragments.

INITIAL MINERALOGY AND NEOMORPHIC CHANGES OF EARLY DIAGENETIC CEMENTS

Modern calcium carbonate cements are formed of aragonite or low- or high-magnesium calcite. Such polymorphic varieties may differ in crystal habits (Schroeder 1972*b*), but fibrous or needle-like crystals seem typical of aragonite, and blade-like or rhombohedral crystals (generally a few μm in size) — of calcite cement (Taylor and Illing 1969, Shinn 1969, Alexandersson 1972, 1973, Evamy 1973, Schroeder 1972b, 1973, MacIntyre 1977, Ginsburg *et al.* 1971, James *et al.* 1976, and others).

Low-magnesium calcite is widely known to be an energetically stable polymorph of calcium carbonate (see Berner 1971b). The high-magnesium variety becomes transformed into the former almost without any change in structure (Bathurst 1980), whereas the passage from aragonite to calcite is connected with change from orthorhombic to rhombohedral crystallographic pattern. In nature the polymorphic transformation of aragonite into calcite may be connected (for review see Carlson 1983) with complete change of original aragonite fabric into calcite sparite (Bathurst 1964, 1971), sometimes pseudosparite (Folk and Asserato 1976, Mazzullo 1980, see also Sandberg 1975), also micrite (Evamy 1973). Combinations of these three forms of secondary calcite may also occur (Taylor and Illing 1969). The change of the original aragonite fabric may be sometimes less drastic (but this is still not agreeded to be a rule — see Kendall and Asserato 1977, Kendall 1977, Asserato and Folk 1980).

Diagenesis of carbonate sediments is usually, but not always, accompanied by their recrystallization, i.e. morphological modification of crystals, not associated with change of mineralogy (for review see Bathurst 1971).

The effects of recrystallization have been found in the hardgrounds under discussion. The most conspicuous effect seen is explosion of primary grains (pl. 14: 1) with disturbance of the original, finely-crystalline internal structure (pl. 14: 2) by crystals of pseudosparite. Within micrites this process leads to a characteristic structure with polygons (somewhat similar to soil polygons) with the centre of a coarser-crystalline aggregate and fine-crystalline rim (pl. 14: 3). With early diagenetic cements this process affects the acicular/bladed fringes. This is unequivocally shown by fringes partly transformed into isometric fringes (pl. 14: 4b), the latter growing at the expense of original grain (pl. 10: 1c). The recrystallization process, in this case, is involved in mineralogical transformation of the acicular/bladed fringes (see next page).

After identifying the effects of recrystallization in these hardgrounds I come back to the question of analysis of the early diagenetic cements. For present purposes two examples of habitat colonization are presented (FO_1, Og_5 — fig. 4), six of pseudo-succession (three of false succession — Og_4, Og_6, V — fig. 4 and three of plausible succession — Og_1, Og_3, M_2 — fig. 5). All examples of broken and true (= autogenic) succession are presented (fig. 6).

Analysis concentrated mainly on partial replacement, metamorphosis and decline of acicular/bladed fringes (Og_1, Og_3, Og_4). In these cases fringes precede micrite cement usually 2—3 cm below the discontinuity (fig. 8).

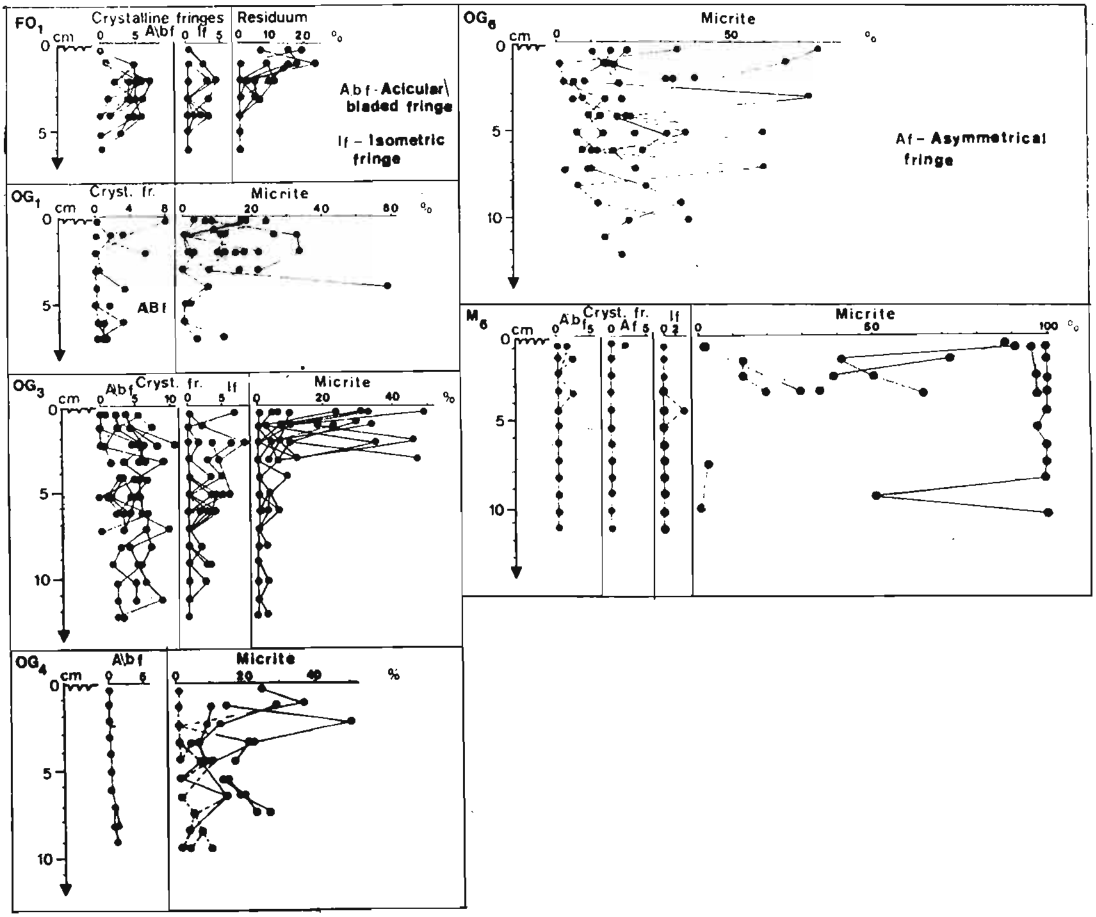

Fig. 8. Occurrence (in per cent of total area of pore spaces) of two types of early diagenetic cements — micrite and crystalline fringes in relation to the hardground surfaces is presented. Relationship between micrite and crystalline fringes is also presented.

The site Og_4 is a special case, because micrite cement extends down to the depth of 10 cm or even 15 cm below the hardground surface (fig. 8).

Metamorphosis of acicular/bladed fringes represented by micritization and alteration into isometric fringes (pl. 14: 4b). When acicular/bladed fringes are partly replaced, pellet-like micrite aggregates are generally situated of on fringe relics (pl. 14: 4a, b) and occasionally directly on grain surfaces (pl. 14: 4a, b). When fringes are entirely replaced, grains are cemented with micrite, microsparite (pl. 14: 5) or fine-grained residual sediment (e.g. FO_1 — fig. 8).

Micritic cement replacing partly or completely acicular/bladed fringes forms meniscus, pendant, gravitational structures, pimple-like overgrowth on grain surfaces. The percentage of micritic cement counting at direct points in relation to the depth away from hardground surfaces (OG_6 — fig. 8) changes suddenly, thus reflecting its patchy distribution (compare Dunham 1971). This unequivocally shows that the cement precipitated under vadose (subaerial) conditions.

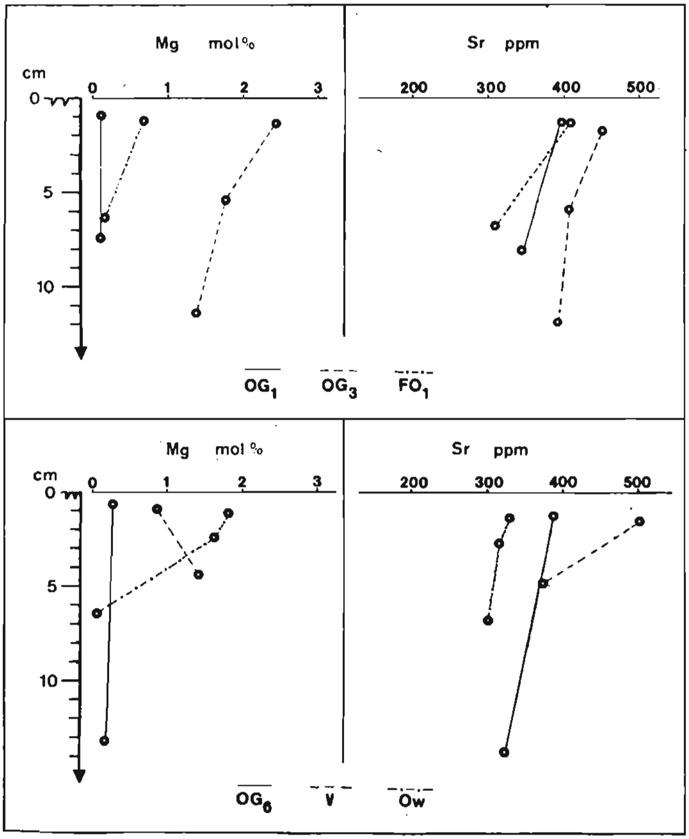

Fig. 9. Sr and Mg content in relation to the surfaces of hardground examples is demonstrated. Note relative increasing of Sr content away from some hardground surfaces.

The decrease in strontium (Sr), which is frequently found with increasing depth below the hardground surface (fig. 9), seems to support the above conclusion. It was noted by Schroeder (1973), Steinen and Matthews (1974) and Pingitore (1976) that under vadose conditions chemical exchange is limited and episodic, thus, the preservation of relics of unstable aragonite is possible, and the leaching of strontium from sediment may not be complete.

Acicular/bladed fringes are better developed below the level at which they coexist with micritic cement. They are characterized by subcrystals, needle-like inclusions in crystals, and non-planar crystal boundaries. Needle-like crystallites (pl. 8: 4) display parallel extinction (abnormal for calcite as it displays oblique extinction).

These features of acicular/bladed fringes and their instability in relation to micrite cement indicate an aragonitic initial mineralogy of the fringes and, at the same time, calcitic mineralogy of micrite. If these fringes were originally built of calcite, subsequent precipitation of either aragonite or calcite micrite would not have led to any of the effects displayed. Transformation of fringes during precipitation of micrite is only possible because they were aragonitic. This also requires a calcitic mineralogy of the micrite.

This process would be impossible if the original mineralogy of the micrite had been aragonite, unless the fringes were built of high-magnesian calcite when transformation of calcite into aragonite (see Milliman 1974) could take place.

By analogy, vadose micritic cement associated with hardgrounds (sometimes also filling burrows and borings), which is not preceded by acicular/bladed fringes (fig. 8, 10 — Og_1, Og_4, Og_6, M_6), was initially calcitic (presumably low-magnesian)[1].

Pellet-like micrite aggregates always present as a major component appear to be identical in structure to vadose micrite (except one special type — Gruszczyński in prep.). Thus, it is difficult to assume that a micritic matrix represents a recrystallized aragonitic mud (see Folk 1965). Following (Sandberg 1975), Loreau (1979) and Gruszczyński and Mastella (in prep.), fine-grained aragonite aggregates become transformed into pseudosparite, sometimes with aragonite inclusions.

Radial elements of some ooids continue within acicular/bladed fringes without any structural defects (pl. 9: 2). Thus, the initial mineralogy of these ooids was partly aragonitic, because of the aragonitic acicular/bladed fringes.

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[1] This would be the exact repetition of the solution-precipitation process, known from modern and Pleistocene carbonate sediments (Bathurst 1971, 1980). In these sediments under vadose conditions: (a) Precipitation of low-magnesium calcite, (b) Transformation of aragonite and high-magnesium calcite into low-magnesium takes place.

The initial mineralogy of coarse, microcrystalline or acicular/bladed-palisade fringes is of minor importance for reconstruction of hardground environment and will be discussed elsewhere (Gruszczyński in prep.).

ANALYSIS OF HARDGROUND ENVIRONMENT

The following analysis was carried with respect to 1) cement stratigraphy, 2) sediment filling burrows and borings, 3) characteristics of the original grains and 4) the skeletal remains. The analysis showed that grains occurring beneath a hardground surface could become completely lithified due to precipitation of a simple sequence of micritic and microsparite cement (fig. 10 — M_2, Pl_3, M_3, M_6). This process began with precipitation of grain-binding micrite, then precipitation of microsparite filling the remaining pore spaces. Partial recrystallization of micrite followed (fig. 10).

The sediment below hardground surfaces generally lithified because of precipitation of several types of early diagenetic aragonite and calcite cements (fig. 10 — Og_1, Og_3). The sequences of aragonitic acicular/bladed fringes which preceded vadose calcite micrite (fig. 10 — Og_1, Og_3, Og_4) indicate the change in sedimentary environment from subaqueous marine to vadose.

Almost all the hardground sequences studied reflect one or more phases of emersion. This is shown by the presence of: (1) asymmetrical fringes within and beyond burrows and borings (fig. 10 — M_3, M_6, and Pl_1, respectively); (2) vadose micrite within (fig. 10 — Og_5, Og_6, Og_4, Og_1, M_6) and beyond (fig. 10 — Og_5, Og_6, V, Og_3, Og_1, Og_4) burrows and borings; (3) corrosional residua which form meniscus, pendant or shoulder-strap structures in (fig. 10 — V, M_2) or beyond (fig. 10 — FO_1) burrows and borings.

Sparry cement cut by borings (fig. 10 — Og_6) or in places replaced by chalcedony or quartz (fig. 10) shows fresh-water phreatic conditions.

Action under fresh-water phreatic or vadose conditions is also indicated (fig. 10) by the mode of shell preservation of gastropods Nerineidae (M_3, Pl_1) adjacent to burrows, and fragments of *Calamophylliopsis* colonies beneath a hardground surface (M_6). The gastropod shells are replaced completely (fig. 10 — Pl_1, M_3; pl. 15: 1a) or incompletely (fig. 10 — Pl_1; pl. 15: 1b) with the same sediment as in the *Thalassinoides paradoxicus* burrows. In the latter case, the part situated furthest of the burrows is occupied by sparry mosaic (fig. 10 — Pl_1; pl. 15: 1c). *Calamophylliopsis* individual corallites have been dissolved at the contact with hardground surface and the voids infilled with sediment identical to that mantling the hardground (fig. 10 — M_6; cf. Roniewicz and Roniewicz 1968).

In almost all the cement stratigraphies and burrow/boring infill stratigraphies (fig. 10) the last stage is denoted by symbols Q or Qr related to precipitation and solution of silica. The process of precipitation of silica (chalcedony or, sometimes, quartz) proceeded in the similar way as the polymorphic transformation of aragonite into calcite (Gruszczyński in prep.). It took place by the dissolution of calcite and precipitation of chalcedony, or by transformation in situ (dissolution of calcite and precipitation of chalcedony/quartz either side of a, sometimes traceable, transformation front — pl. 15: 4). This process is marked by the replacement of several calcite nuclei of pellet-like micritic aggregates, disturbances of primary structures in calcite shells (pl. 16: 1), and small-scale destruction of calcite crystals forming the inner fringe within voids (e.g. empty interior of a shell) (pl. 16: 2). In the latter case quartz continued to crystallize in the void, thus burying the calcite fringe (pl. 16: 2). Single crystals of chalcedony/quartz in a sparite filling within and outside boring were also found. Chalcedony and quartz fringes replacing sparite mosaic occur in voids in burrows and borings (fig. 8 — M_2; pl. 16: 5).

Solution of chalcedony/quartz may be complete, but sometimes relics of silica or opaque ferrous matter may remain (fig. 10 — M_6; pl. 16: 3, 4).

Evidence of early diagenetic precipitation and solution of silica is shown by: (i) chalcedony/quartz found only just beneath hardground surfaces (fig. 11), and (ii) etched quartz occurs mainly in incompletely-filled burrows, borings, and voids (pl. 12: 3c), indicating subaqueous marine post-omission conditions favourable for precipitation of calcium carbonate.

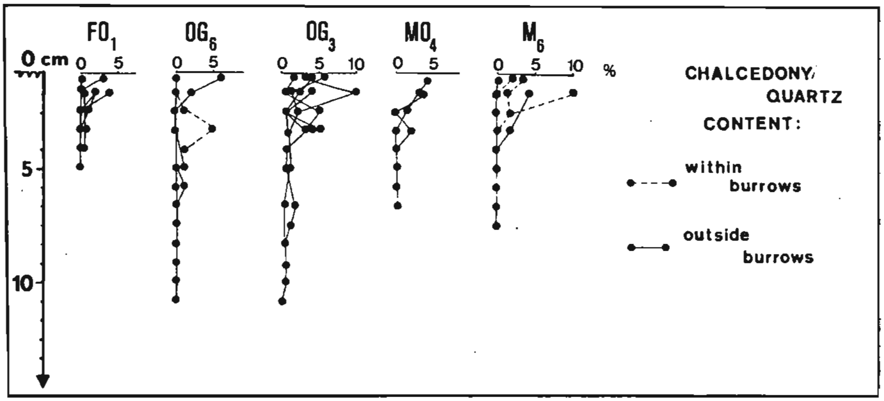

Fig. 11. Occurrence of quartz and/or chalcedony (in per cent of total area) in relation to the hardground surfaces. Note the generally decreasing content of quartz and/or chalcedony away from the hardground surfaces.

The available analytical data was subsequently used to reconstruct the varying environments of individual hardgrounds and to evaluate the eventual influences on the ecological succession of benthic associations.

EARLY DIAGENETIC HISTORY OF HARDGROUNDS

The early diagenetic history of hardgrounds comprises events from the onset of bottom colonization under conditions of waning deposition till burial (fig. 12): it is the record of associations replacement including habitat colonization and pseudo- (false and plausible) succession, broken and true (= autogenic) succession examples.

The hardground formations with the record of habitat colonization appear in complex image of the history in the second scene. This stage includes either cementation under subaqueous conditions and the succeeding colonization (FO_1 — fig. 12) or cementation under vadose conditions (Og_5 — fig. 12). The latter was followed by colonization only after a return to subaqueous marine conditions (Og_5 — fig. 12) and one more emersion (fig. 12). In the last stage of development, the hardground sequences became influenced by waters with low pH under vadose (FO_1 — fig. 12) or fresh-water phreatic (Og_5 — fig. 12) conditions.

Hardground sequences with false successions appear early in stratigraphy (fig. 12). They correspond to the colonization of loose sediment under waning rates of sedimentation. The next events include colonization of the seafloor lithified or subaqueous marine cementation (Og_4, V — fig. 12) or cementation under vadose (subaerial) conditions (Og_6 — fig. 12). The next stages are additionally related to either emersion of some hardgrounds (Og_4 — fig. 12; Og_6 — fig. 12) or the continued submersion of the remaining ones (V — fig. 12). The last stage connected with the influence of low pH waters on all the three hardground formations under vadose conditions (Og_6 — fig. 12), or conditions changing from vadose to fresh-water phreatic (V — fig. 12) and phreatic (Og_4 — fig. 12).

Hardground recording plausible successions appear in the first (Og_1, Og_3 — fig. 12) and second (M_2 — fig. 12) stages, i.e. those related to the colonization by benthic organisms of initially loose (Og_1, Og_3) and, thereafter, cemented substrates (Og_1, Og_3, M_2). This was followed by one (Og_1 — fig. 12) or two emersions (Og_3 — fig. 12), or continuation of subaqueous marine regime (M_2 — fig. 12). The last stage is connected with the influence of waters of low pH on the hardground formations under environmental conditions changing from vadose to fresh-water phreatic (M_2, Og_1 — fig. 12) or phreatic conditions (Og_3 — fig. 12).

Hardgrounds exhibiting broken and true successions appear in the first stage (fig. 12). They pass through the stage of colonization of cemented bottom (fig. 12), and remain under subaqueous marine conditions till their burial. During their burial history they were subjected to low pH under vadose (fig. 12), varying vadose-phreatic (fig. 12) or phreatic (fig. 12) conditions.

The history of the hardgrounds suggests that the drastic changes in chemistry, related to changes in environment, from subaqueous marine to vadose or fresh-water phreatic conditions could be responsible for breaking the ecological succession. However, ecological succession could not occur except under continuing subaqueous marine conditions. This made it necessary to look for other factors influencing development of ecological succession in fully reconstructed environments of hardground formations.

Regardless further analysis, I would like to note that environmental conditions were unusually severe for benthic organisms associated with hardgrounds judging from the composition of the biota. Pioneer colonizers — burrowers as well as late successional dominants — borers and encrusters are aggregated in clusters, distributed over limited area and numerically dominating the fossil associations by over 80% in numbers, thus can be regarded as opportunistic (Levinton 1970). This indicates, again, the unstable environment of high physiological stress and implies the explanation of decrease in diversity of examined biota in comparison with the other Jurassic hardgrounds (e.g. Fürsich, 1979, Palmer 1982).

The list of boring and encrusting forms recorded in upper Jurassic hardgrounds in the Holy Cross Mts. is fairly short in comparison with those reported from other hardgrounds in the Jurassic of Europe (cf. Fürsich 1979), as it contains 10 times less taxa. In turn, markedly more boring bivalves in the Holy Cross Mts. hardgrounds than in any other Jurassic omission surface formations in Europe (cf. Fürsich 1979) have been found.

The last successional species are dominated by boring bivalves of the family Mytylidae, characterized by a wide range of adaptation possibilities. The bivalves could: (1) not only bore but also browse in loose deposits, (2) use free shelters (empty borings) and crevices in the bottom for nestling without making any borings, (3) produce calcareous siphonal linings (cf. Yonge 1964), protecting a boring from burial by incompletely lithified subsurface deposit. The adaptation possibility (3) is, therefore, not of zootaxonomical significance (see Kelly and Bromley 1984). (Kelly and Bromley (1984) maintained that some species of boring bivalves are incapable of secreting calcareous linings).

PALEOGEOGRAPHY

The stratigraphy, sedimentology, and paleogeography of the area were studied by Kutek (1968, 1969). From petrographic and sedimentological analysis, and comparisons with modern carbonate sedimentary environments he interpreted the hardgrounds associated sediments as having been deposited in a shallow (locally, extremely shallow) marine basin. He also stated that the Holy Cross Mts. could not have represented a separate paleogeographic unit, contrary to earlier interpretations, in which this area was shown as land (see e.g. Książkiewicz *et al.* 1965). Kutek (1969), in proposing his model referred to the lack of intertidal, dolomitic and other facies which would indicate emergent areas during the Oxfordian and Kimmeridgian. However, he did not exclude the existence of ephemeral islands during periods of oolite production, which he compared with modern, carbonate deposition on the Bahama platform (Ball 1967). As for the hardgrounds, he did not agree with Kaźmierczak and Pszczółkowski (1968) who assumed that the hardgrounds were formed at stress of subsidence stillstand, leading to extreme shallowing and, therefore, breaks in carbonate deposition. Kutek (1969) rejected this assumption referring to the lack of evidence for uplift or eustatic sea-level changes in the area.

The available data is insufficient for an unequivocal statement whether or not the Holy Cross Mts. was emergent in Latest Oxfordian and Early Kimmeridgian times. The statement that this area was submerged, made on the basis of a few sedimentary features from adjacent areas and extrapolation of the thickness of Mesozoic strata adjoined Paleozoic core of the Holy Cross Mts. (Kutek and Głazek 1972), is difficult to accept, especially because of the evidence presented above for the existence of land areas in Late Oxfordian and Early Kimmeridgian times. It should be also noted that these temporarily emergent areas were situated close to a *terra incognita*, i.e. the present Paleozoic basement of the Holy Cross Mts. I think that during this period the Holy Cross Mts. formed a transitional, continental-marine zone (fig. 13B) with mixed carbonate and swampy facies but not necessarily dolomitic or anhydritic, as in SE Poland (fig. 13A).

Taking into account the results of studies on Oxfordian and Kimmeridgian strata of the Polish Jura Chain (A. Wierzbowski and B. Matyja, pers. inf.) the zone under discussion passed into open sea (fig. 13A). This seems to give further support for the above interpretation of the zone as marginal to a transitional, continental-marine area (fig. 13B).

As to the origin of the discontinuity surfaces, although it appears complex it is impossible to ignore temporary heets to subsidence, eustatic sea-level changes, and movements of the sea floor.

It follows that the shoal was divided into more or less isolated basins by islands, barriers and bars (fig. 13B) which changed in migrating position with time. This is seen by the distribution of hardgrounds that must have emerged (fig. 12).

The occurrence of evaporites in the Upper Oxfordian and Kimmeridgian of SE Poland (fig. 13A; Niemczycka 1976) does not seem to indicate that the whole area of Poland necessarily belonged at that time to the arid zone (Hallam 1984).

The studied strata display some structures resembling plant detritus as well as leaves possibly of cycads. Coeval strata to the north yield *Zamites gigas* (Premik and Zabłocki 1921). Remains of cycads, bennettites, cordaites, horsetails discovered by Liszkowski (1972), within Oxfordian strata indicate humid conditions at that time. This supported by paleomagnetic data (Barron *et al.* 1981) indicating that Poland was situated in the tropics in the Oxfordian and Kimmeridgian. Therefore, it cannot be excluded that the area was repeatedly subjected to extended rainy seasons which would have resulted in freshening parts of the basin. Heavy rain would result in decreasing salinity and also in a lowering of pH because of the introduction of humic acids.

Individual island-delineated basins could be completely isolated, evidence for which can be the appearance of two generations of calcium carbonate — replacing silica: one, represented by grey chalcedony or megaquartz (see Folk and Pittman 1971), and the other — by translucent fine crystals of authigenic quartz (pl. 15: 2b). I interpret the first generation as evidence of decrease in salinity and lowering of pH of waters in a basin, and the second as possibility related to an increase in salinity to higher than normal marine (see Folk and Siedlecka 1974).

On the basis of this outline image of a part of upper Jurassic basin I made an attempt to reconstruct conditions of life of benthic organisms.

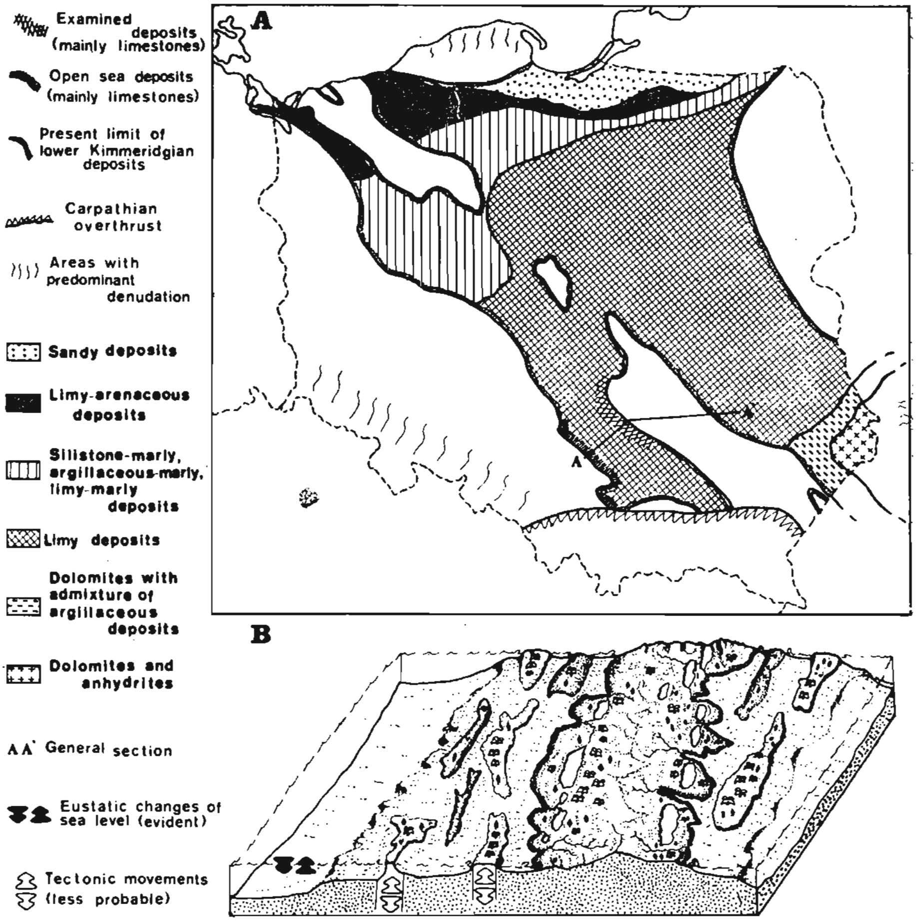

Fig. 13. General palaeogeography of studied area. *A* General facies map of Poland of Early Kimmeridgian times is adopted from Dadlez *et al.* (1964) and Niemczycka (1976). The studied area is situated close to the present Paleozoic basement of the Holy Cross Mts. *B* General section AA′ marked in a facies map is showed. Presented blockdiagram is mainly a product of author's imagination.

GENERAL FACIES/ENVIRONMENTAL INTERPRETATION

When the hardgrounds sequences are viewed against the whole upper Jurassic succession they can be seen to be concentrated at a few, relatively thin intervals (fig. 14A). These intervals were analyzed using sedimentological rules dealing with the siliciclastic deposition (fig. 14A). The data made it possible to present five probable depositional models (fig. 14—17). These models may be briefly characterized as follows (from facies characteristics of the oldest sediments to the youngest):

Model I — A detached shoal (fig. 15A) whose separation was possibly due to the presence of barriers or barrier islands built of coarse (oolitic) deposits (fig. 15C). Current and wave activity took place at the shoal margins (fig. 15A) whilst fine-grained sediment accumulated on the shoal itself. Deposition, continuing under fair weather conditions, was intermittent, most probably because of stroms (see Kelling and Mullin 1975). Such a deposition is reflected in the benthic world yield redeposition of organic remains (fig. 15A). The available data suggests that hydrodynamic activity was not high at sites of potential hardgrounds (fig. 15B).

Sedimentation and cementation rates were presumably sufficiently low (fig. 15B) benthic communities to become established. A decrease in the sedimentation rate is shown by the close packing of micritic pellets or pellet-like aggregates, associated with an increase in frequency of nerineid gastropods.

Model II — A flat sea floor (fig. 16), with local small elevations (fig. 16C), resembling tidal flats (see for review Reineck and Singh 1973). It was a place of deposition of fine-grained (pellet-like micrite aggregates) sediment, disturbed by weak wave and current reworking (fig. 16A). It follows that hydrodynamic activity was not high at this early stage of hardground formation M_3 (fig. 16B). Deposition and cementation rates were also low, which is shown by the lack of intraformational, ephemeral hardgrounds, so common elsewhere (fig. 16A). These rates were suitable for free development of the benthic biota (M_3 — fig. 16B).

This pattern was followed by the common appearance of shore and nearshore facies (fig. 16A; Clifton *et al.* 1971). The latter were characterised by numerous belts of rip current channels and fans (fig. 16A, C). The sea floor was locally emergent (fig. 16C) which resulted in the appearance of beach and backshore facies (fig. 16A). The seafloor up to several km from the shore was gently sloping, with underwater ridges, longshore bars and runnels (fig. 16C). At times of hardgrounds FO_1, V, and MO_4 development, hydrodynamic activity could be moderately high (fig. 16B), whereas rates of deposition and cementation were very variable. It may be assumed that these rates were moderate in the case of hardground MO_4, and fairly high in hardgrounds V and FO_1 (fig. 16B). Hardground FO_1 was formed within shore and nearshore facies (fig. 16A) which makes the situation clear. High rates of sedimentation and cementation (fig. 16B) are evident at site V from traces of bivalve excape structures and the presence of ephemeral hardgrounds.

Model III — A belt of oolitic shoals with a system of migrating and often emergent bars (fig. $14C^+$). This is the only possible interpretation of sedimentary structures represent mega-cross bedding (fig. $14A^+$), indicative of strong wave and wave-induced current reworking, thus indicating high hydraulic energy (fig. $14B^+$ — Og_6). The rate of deposition was probable high (fig. $14B^+$) with conditions inhospitable to colonization.

Model IV — A shoal which may be divided into two parts:

(i) an open shoal with numerous elevations (fig. 17C), partly emergent

(OG_5 — fig. 12) and with bottom sediments actively reworked by waves and currents, except areas between the elevations (fig. 17A); and

(ii) a shoal with relatively fewer fine-oolitic belts proximally, was responsible for the stagnant and isolated character of some basins (fig. 17C), shown by changes in water in one of the basins from fresh to hypersaline (M_2 — fig. 12). In the proximal part of the shoal, beyond fine-oolite belt, quiet deposition in partly isolated basins was often disturbed (fig. 17A) by storms (see Goldring and Bridges 1973); see also Johnson 1978). In its distal part (fig. 17A) deposit there was occasional reworking. Thus, hydrodynamic activity was variable allowing rich benthic biota development and formation of numerous ephemeral omission surfaces (fig. 17B — M_6).

Model V — A shoal with a system of stagnant oolite belts and rarely migrating bars (fig. 14C) seems to be the most likely interpretation of the coarse (oolitic) sediment mixed with fine-grained (micritic pellet-like aggregates). The sediments occasionally display parallel lamination and rarely mega-cross bedding units (fig. 14A) indicating deposition mainly from suspension, beyond influence of decelerating currents. In some places the deposition changes to bed load related to the activity of waves and wave induced currents.

Hydrodynamic activity was variable but generally moderate at hardground sites Og_1, Og_3, and Og_4, and low at Ow (allowing free development of benthic biota) (fig. 14B). The rates of deposition and cementation were estimated from: (i) the presence of undefined burrows deep below the hardground surface (Og_1, Og_3, Og_4 — fig. 14B); (ii) lack of ephemeral hardgrounds.

It follows from the above analysis that additional factors which may control the ecological succession include hydrodynamic activity and rates of deposition and cementation. When these attain large values, an ecological succession lacking (fig. 14—17). When the values are low, an ecological succession may be detected, as at, M_3, M_6, O_w, Pl_1.

CONCLUSIONS

In this paper I have analyzed the question of the applicability of the concept of the ecological succession (sensu Odum 1969, i.e. "facilitation" model by Connell and Slatyer 1977) for ancient sedimentary omission sequences, in particular numerous hardgrounds from the Oxfordian-Kimmeridgian passage beds in the Holy Cross Mts. The record of the succession of benthic associations associated with these hardgrounds was tested against the three parameters of ecological succession.

I distinguished: (i) association replacement including (1) habitat colonization, unrelated to succession of benthic associations, (2) pseudosuccessions divided into false succession, that fails to show any feature of ecological succession, and plausible succession matching only the first parameter; (ii) autogenic successions embracing (1) broken succession, matching the first and second parameters, and (2) true succession, matching all three parameters.

The hitherto accepted model of ecological succession in hardground formations (Goldring and Kaźmierczak 1974) considered only the first parameter, concerning the ordered and directional development of an ecosystem. It comprises true succession as well as pseudo- and broken successions, so cannot be regarded as completely valid.

In an attempt to identify environmental factors responsible for origin of the ecological succession in hardgrounds I reconstructed the early diagenetic history of selected hardgrounds and, on the basis of this, a general paleogeographic model for the overall area. Subsequently I made an attempt to characterize the environmental settings for these selected hardgrounds. It has been possible to identify a few factors which control the ecological succession, such as hydrodynamic activity (waves and currents), changes in salinity, pH, waters chemistry, and rates of deposition and cementation.

The early diagenetic history shows that the majority of the studied hardgrounds were subjected to emersion due to impedance of subsidence and/or eustatic changes of sea level. Some (fig. 12) were repeatedly subjected to emersion indicating frequent eustatic sea-level changes and/or synsedimentary movements of the sea-floor. Exceptionally, the burial phase of hardgrounds was followed by temporary decrease in salinity in some parts of the basin. In the burial phase, decrease in salinity in particular basins as was accompanied by decrease in pH and acidification.

Drastic changes in the abiotic environment resulted in decrease in diversity of hardground biotas in comparison with other Jurassic hardgrounds and wide range of adaptation possibilities among the boring bivalves. Such unstability of the environment caused opportunistic pioneer colonizing species well as late successional dominating species.

It seems likely that the overall area studied was a wide shoal, with water depth no greater than 10—15 m and sea-floor elevations of the order of a few meters. The platform was divided into a number of zones, sometimes isolated by temporarily emergent islands, barriers, bars or oolite belts. These migrated in time and space, resulting in changes in facies distribution and sites of hardground initiation.

Differences in colonization of hardground surfaces and burrow networks (in the case *Thalassinoides paradoxicus* burrows), also found in other Jurassic hardgrounds (Palmer and Fürsich 1974, Fürsich and Palmer 1975) were due to a weaker circulation within burrows. This was a reason for the decrease in food supply and poisoning of burrow environment with products of metabolism and, therefore, possibly in high mortality of juvenile boring bivalves.

The process pattern of replacement of calcite by chalcedony/quartz is similar to the polymorphic transformation of aragonite into calcite. The transformation of calcite into quartz may take place through either dissolution of calcite, followed by precipitation of chalcedony in the same place, or alteration *in situ*, connected with dissolution of calcite on one side of sometimes traceable alteration front, and precipitation of chalcedony/quartz on the other.

Environmental changes proceeding in time of formation of hardgrounds resulted in prolonged activity of calcium carbonate solution-precipitation process and, therefore, possible to complete syngenetic lithification of subsurface hardground formations prior to their final burial. This makes possible studies on origin and initial mineralogy of a wide range of carbonate grains.

Activity of solution-precipitation process resulted in origin of carbonate cements differing in crystal habit and mineralogy. The cements were originally aragonitic as well as calcitic but the question whether this was low- or high-Mg calcite remains open. It should be noted that cements identical in mineralogy but differing in crystal fabrics as well as those differing in mineralogy could originate in the same microenvironment (see Gruszczyński in prep.). Similar phenomena are known from modern marine environments (see Bathurst 1980). Similarly as in the latter, cementation appears best developed in intragranular pores (especially inside shells of Nerineidae gastropods) in the studied hardground formations, a replacement of aragonite fringes by calcite micrite is found, and the studies show that upper Jurassic ooids originally had aragonite structural elements. It follows that chemistry in the studied part of the Late Jurassic basin was not much different from that of modern sea water as suggested by Loreau (1978, 1979) or Sandberg (1983).

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Appendix I

The degree of substrate lithification associated with each taxon was made using criteria proposed by Goldring and Kaźmierczak (1974, outline of burrows and borings, sediment filling these structures and mutual relationships, shape of boring bivalve shells, and appearance of hardground surface) supplemented by three other criteria (Gruszczyński 1979): (i) borings in sediment infilling older burrows and borings indicating lithification of the sediment (cutting grains and matrix/cement equally), (ii) oysters attached, to but slightly pressed into the substrate, indicating incomplete lithification; the oysters (depending on genus), which spread out over the substrate accurately taking up (xenomorphocially) the morphology of the substrate, or attaching to it with a small portion of shell, indicate complete lithification, (iii) tubular crystalline linings protecting apertures of borings, indicate colonization of a loose substrate.

Appendix II

Description of organisms and organic structures (listed below) associated with examined hardground formations.

(1) Undefined burrows — irregular in outline and usually indistinct, mm-cm diameter.

(2) Bivalve burrows — showing evidence of escape (pl. 1: 1) and others, showing adjustment (pl. 1: 2).

(3) Other bioturbation structures — including structures surprisingly similar to burrows of the Recent echinoid *Echinocardium cordatum* or polychaete *Pectinaria coreni*, or sipunculids and priapulids (see Schäfer 1972, pl. 1: 1). However, the fossil structures cannot be assigned to definite ichnogenera because a single organism may make trails of various types.

(4) U-shaped tubes characterized by fairly thick (1—2 mm) calcareous walls which protected the animal from burial by loose deposit. The tubes are < 0.5 mm in diameter with openings at 2—3 cm apart, and reach a depth of 2 to 3 cm. U-shaped tubes are made by several animals but here we are dealing with an animal which secreted calcium carbonate tube most probably a representative of the family Serpulidae.

(5) Burrows of *Thalassinoides* type, assigned to *Thalassinoides paradoxicus* (= *Spongelimorpha paradoxica*) and *Thalassinoides suevicus* (= *Spongelimorpha suevica*) (Kennedy 1967, Fürsich 1973b). Burrows 0.5 to 2 cm in diameter, irregular in course, and repeatedly interlacing and crossing one another are classified under *Th. paradoxicus*, and those usually 0.5 to 1 cm in diameter and regular in course, with numerous rectilinear sections and occasional branchings under *Th. suevicus*. This differs somewhat from the characteristics of the two taxa as given by Ekdale and Bromley (1984).

Burrows of *Th. paradoxicus* (pl. 2: 1) seem to be mainly related to loose sediment, since the burrow outlines are markedly deformed by compaction (pl. 2: 1a). Grains are usually displaced and only occasionally cut (pl. 2: 1c). However, burrows with slightly deformed outline, though rare, show that the organisms responsible could also penetrate firm sediment (pl. 2: 1b).

Burrows of *Th. suevicus* penetrated firm ground, which is shown by undeformed burrow outlines (pl. 2: 2a, b), and by truncation of both sediment grains and, locally, matrix. In some sections the burrows appear deceptively similar to those of modern *Callianassa* (Shinn 1968, Schäfer 1972).

(6) Burrows of *Arenicolites* type — U-shaped, extending to 5 cm below firm ground surface and usually 0.5 to 1.5 cm in diameter, resembling the burrows of *Corophium* of or *Echiurus* (Reineck and Singh 1973).

(7) Single burrows representing three morphotypes:

(i) straight to slightly curved burrows penetrating almost normal to bedding (pl. 3: 1), and extending to a depth of 8 cm. The burrows, up to 2 cm in diameter, somewhat resemble those of some modern crabs described from the Bahamas (Shinn 1968) those of *Uca* (Basan and Frey 1977) or *Ocypode* (Frey *et al.* 1984). However, the available material is too limited for allocation to definite ichnogenera, e.g. *Psilonichnus* (Frey *et al.* 1984).

(ii) short and branching L- or T-shaped burrows (pl. 3: 2) extending to 2 cm and up to 0.5 cm in diameter near openings.

(iii) irregular burrows, usually with a wedge-like ending (pl. 3: 3) up to 3 cm long and about 0.5 cm in diameter near openings.

Comparison of types (ii) and (iii) with modern burrows seems risky, despite the similarity of type (iii) to modern sipunculid burrows.

(8) Boring bivalves, mainly of the genus *Lithophaga* (pl. 3: 4), as well as *Gastrochaena* (pl. 3: 5) of the family Mytilidae. When borings do not contain shells of these bivalves, but appear identical in shape as those with shells, they may be conventionally referred to *Lithophaga*-like or *Gastrochaena*-like. Both forms are associated with many others, which should be defined as boring of bivalves "X" or "X"-like because bivalve remains appear impossible to separate from the rock. Shells of bivalves "X" are almost circular in cross-section, with the length-width ratio varying from 0.9 to 1.1. Moreover, a single boring somewhat similar to that of bivalves *Jouanetia* has been found.

According to ichnological nomenclature by Kelly and Bromley (1984) *Lithophaga*-like and *Gastrochaena*-like borings have to be assigned to *Gastrochaenolites lapidicus*, whereas "X"-like borings have to be classified under *Gastrochaenolites orbicularis*. The *Jouanetia-like* borings have to be assigned to *Gastrochaenolites lapidicus*.

(9) Borings of *Trypanites*-type are represented by two morphotypes;

(i) straight to slightly sinusoidal tubes (pl. 4: 1a, b, c), 0.1 to 0.3 cm in diameter and up to 6—8 cm or even 15 cm long probably made by polychaetes and assigned in the literature to *Trypanites weisei* (Bromley 1972).

(ii) short tubes (1—2 cm long) with sharp or U-shape termination (pl. 4: 2), 0.1—0.3 cm in diameter, and similar to those of Recent polychaetes *Polydora* (*P. ciliata*) or *Potamilla* (see Holder and Hollman 1969, Schäfer 1972).

(10) Rare single and simple borings:

(i) short borings (about 3 cm long) with expanded drop-like termination endings (pl. 4: 3) which may be due to polychaetes,

(ii) straight (up to 8 or even 10 cm long) tubes, slightly bent or wedge-like at the end (pls. 4: 4, 5: 1), similar to those of the Recent sipunculid burrows,

(iii) bell-like crypts with narrow (2—3 mm) opening with the depth of 2 cm (pl. 5: 2), similar to burrows of Recent echinoids *Echinocardium cordatum*. Borings representing the two latter morphotypes are rather rare, so they are not given formal names but referred to as burrows of Sipunculida and Echinoidea.

(11) Encrusting oysters are represented by *Nanogyra* (*N. nana*) and *Liostrea* (pl. 5: 3a, b). The latter attaches to firm and hardground (pl. 5: 3); the former encrusts fully lithified substrate.

(12) Traces of attachment of pedicles of three species of brachiopods are common: *Zeilleria humeralis*, *Epithyris subsella*, and *Septaliphoria pinguis*;

(13) Encrusting serpulids (see Fürsich 1979, Palmer 1982):

(i) *Cycloserpula* (most common, somewhat resembles *Propomatoceras dentata* — Ware 1975) with tube circular in cross-section (pl. 5: 4);

(ii) *Tetraserpula* (somewhat resemble *Flucticularia sharpei* — Ware 1975) with tube rectangular in cross-section, and

(iii) *Dorsoserpula* (resembles *Propomatoceras keepingi* — Ware 1975), with tube circular in cross-section and a suture clearly visible on its surface.

(14) Laminated, stromatolite-like (columnar or mat-like) structures (pl. 13: 2a), are best developed upon upper portions of the *Thalassinoides paradoxicus* burrows (pl. 13: 1, 2a). I observed numerous bivalve borings within these structures. Borings which cut through older lamine but may not continue into younger layers indicate that the laminated structures were cemented *in statu nascendi*.

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SUKCESJA EKOLOGICZNA W WARUNKACH WCZESNEJ DIAGENEZY GÓRNOJURAJSKICH OSADÓW WĘGLANOWYCH Z GÓR ŚWIĘTOKRZYSKICH (POLSKA)

Streszczenie

Sukcesja ekologiczna jest pojęciem dotyczącym rozwoju biocenoz, a wynikłym z obserwacji przekształcających się ekosystemów. Jako mechanizm rozwoju biocenoz, charakteryzuje się ona określonymi prawidłowościami. Ostateczne ustalenie tych prawidłowości przypisuje się Odumowi (1969). Te prawidłowości to: 1) kierunkowy i uporządkowany rozwój biocenozy obejmujący określone zmiany składu gatunkowego biocenoz w czasie; 2) zmiany te wynikają ze zmian środowiska wywołanych przez biocenozę, powodując inwazję nowych, lepiej przystosowanych do życia w zmienionym środowisku gatunków, a wymieranie gatunków powodujących te zmiany lecz przystosowujących się z trudem do tych zmian; 3) punktem kulminacyjnym rozwoju jest ekosystem ustabilizowany, w którym utrzymuje się równowaga pomiędzy biocenozą a środowiskiem abiotycznym.

W związku z tym, że sukcesja ekologiczna jest pojęciem teoretycznym, przedstawione tu prawidłowości są idealizacją procesów zachodzących w naturalnych środowiskach i znajdują one potwierdzenie tylko w obrębie małych, izolowanych ekosystemów (Odum 1971). Toteż koncepcja prezentowana przez Oduma była wielokrotnie rewidowana, głównie przez biologów. Obecnie, dość powszechnie, przyjęło się wyróżniać trzy modele sukcesji ekologicznej (Connell and Slatyer 1977), z których jeden jest równoważny z koncepcją Oduma.

Próby zastosowania modeli sukcesji ekologicznej do kopalnych zespołów organicznych, głównie bentosowych, zwykle kończą się niepowodzeniem, szczególnie jeśli rozpatruje się następstwo zespołów na przestrzeni kilku czy kilkunastu milionów lat (Bretsky i Bretsky 1975, Walker i Alberstadt 1975).

Po krótkich rozważaniach, można dojść do wniosku, że tylko model tzw. „ułatwiający" (Connell i Slatyer 1977) — odpowiednik koncepcji Oduma (1969) da się odnieść do kopalnych zespołów bentosowych. Zawężenie badań do horyzontów krótkoczasowych z dobrze zachowanymi pozostałościami po organizmach bentosowych pozwala, w pewnym stopniu, na stwierdzenie sukcesji ekologicznej w stanie kopalnym.

Zaadaptowane, do wymogów stanu kopalnego, prawidłowości, czy parametry sukcesji ekologicznej wykorzystano do stwierdzenia istnienia zapisu sukcesji w strefach synsedymentacyjnie cementowanego osadu dennego, tj. twardych den.

Korzystając z modelu sukcesji ekologicznej w twardych dnach, zaproponowanego przez Goldringa i Kaźmierczaka (1974), skonstruowano szeregi sukcesyjne dla każdego z 33 badanych, górnojurajskich twardych den. Był to test na zgodność zapisu następstwa kopalnych zespołów bentosowych z pierwszym kryterium sukcesji, czyli o uporządkowanym i kierunkowym rozwoju asocjacji organicznych. Okazało się, że w kilkunastu zrekonstruowanych szeregach brak jest kilku poszczególnych ogniw w szeregach sukcesyjnych. Przypadki te zostały tu zakwalifikowane jako przykłady kolonizacji dna i fałszywej sukcesji. Nie mają one nic wspólnego z sukcesją ekologiczną lecz są jedynie następstwem zespołów bentosowych.

Przypadki spełniające pierwsze kryterium sukcesji poddano testowi na zgodność z drugim z kolei kryterium, rozumiejąc tu zmianę środowiska abiotycznego jako twardnienie osadu dennego. Poszukiwano syngenetycznych cementów węglanowych bezpośrednio związanych z aktywnością życiową asocjacji pionierskiej tzn. zespołu organizmów ryjących.

Spośród kilkunastu typów wczesnodiagenetycznych cementów jedynie cztery były bezpośrednio związane z działalnością pierwszych kolonizatorów dna. Po wyróżnieniu tych typów cementów we wszystkich analizowanych przypadkach, okazało się, że jedynie siedem stref twardych den z zapisem następstwa zespołów bentosowych obfituje w wyróżnione cementy.

Wobec tego, oprócz wcześniej wymienionych, istnieje również sukcesja pozorna reprezentująca następstwo asocjacji bentosowych, które spełnia pierwsze kryterium sukcesji ekologicznej. Powoduje to także ograniczenie stosowalności modelu Goldringa i Kaźmierczaka (1974), gdyż spełnia on tylko wymogi pierwszego kryterium sukcesji.

Trzecie kryterium sukcesji, czyli maksymalny rozwój ostatnich, w szeregu sukcesyjnym, mieszkańców skamieniałego dna morskiego eliminuje trzy z siedmiu pozostałych stref twardego dna.

Wynika z tego, że w czterech z wielu badanych stref twardego dna, zapis następstwa asocjacji bentosowych spełnia wymogi sukcesji ekologicznej.

W poszukiwaniu czynników ograniczających czy uniemożliwiających istnienie sukcesji ekologicznej w tych strefach, dokonano rekonstrukcji środowiska twardych den.

Stwierdzono, że wiele z nich wynurzało się, niekiedy wielokrotnie, w czasie swojego rozwoju, były poddawane działalności agresywnych wód słodkich, a wszystkie u schyłku swojego istnienia zmieniane były wskutek zakwaszenia wód.

W szerszym kontekście paleogeograficznym twarde dna stanowiły elementy rozległej płycizny, o głębokościach do kilkunastu metrów, podzielonej na liczne akweny przez migrujące w czasie i przestrzeni wyspy i bariery.

Było to środowisko niezbyt przychylne bujnemu rozkwitowi zespołów bentososowych, co odzwierciedla się w niezwykle małej różnorodności fauny stowarzyszonej z badanymi twardymi dnami w porównaniu z równowiekowymi odpowiednikami w innych częściach Europy.

Praca została wykonana w ramach problemu MR II 6.

EXPLANATION OF PLATES 1—21

Plate 1

Organic structures representative for the first and the second link of the order of succession.

1. Trails (ET) of escaping bivalve are clearly visible. Bioturbation structures (BS) resembling those of Recent echinoids, polychaetes, priapulids and sipunculids are also visible. These structures point out the stage of loose bottom sediment. They belong to the pioneer association — the first link of the order of succession. Cross-section of *Thalassinoides suevicus* (Ts) burrow points out the stage of firm ground. *Thalassinoides suevicus* belongs to the second link of the order of succession. Slab of the V hardground — Występy.
2. Bivalve trails (BT) point out the stage of loose bottom deposit. Burrowing bivalves, therefore, producers of such trails belong to the pioneer association — the first link of the order of succession. Slab of the M_5 hardground — Góra Skorkowska.

Plate 2

Organic structures representative for the first and the second link of the order of succession.

1a. Network of *Thalassinoides paradoxicus* burrows. Deformed outlines of the burrows point out the stage of loose bottom sediment. This *Thalassinoides paradoxicus* belong to the pioneer association — the first link of the order of succession. Slab of the Pl_1 hardground — Góra Kluczowa 1.

1b. Slightly deformed outline of *Thalassinoides paradoxicus* burrow points out the stage of firm ground. This *Thalassinoides paradoxicus* belongs to later colonizers association — the second link of the order of succession. Slab of the M_3 hardground — Lipia Góra.

1c. Thin section shows *Thalassinoides paradoxicus* burrow cross-section. Relationship between outline of burrow and deposit grains is visible. The outline of burrow only sporadically cut the grains (arrow). Slab of the Op_2 hardground — Góra Chojny.

2a. Network of *Thalassinoides suevicus* burrows is similar to that of Recent *Callianassa* shrimps. Slightly deformed outlines of the *Thalassinoides suevicus* burrows point out the stage of firm ground. The *Thalassinoides suevicus* belongs to the later colonizers association. Slab of the M_2 hardground — Rogalów.

2b. Cross-section perpendicular to the network of *Thalassinoides suevicus* burrows shows slightly compacted outlines of burrows. This emphasizes position of the *Thalassinoides suevicus* among association repreentative for the second link of the order of succession. Slab of the M_{10} hardground — Sobków.

Plate 3

Organisms and organic structures representative for the second and the third link of the order of succession, i.e. belonging to the later colonizers and late successional dominants associations.

1. Single burrow — morphotype I. Long, straight or slightly undulated burrow. Slab of the M_{MO_2} hardground — Występy.
2. Single burrow — morphotype II. Short and T branching burrow. Slab of the MO_3 hardground — Góra Skorkowska.
3. Single burrow — morphotype III. Irregular outline of chiselended burrow. Slab of the Pl_1 — Góra Kluczowa 1.
4. *Lithophaga* bivalves in their borings. Slab of the M_6 hardground — Brzegi.
5. Cross-section of the *Lithophaga* and *Gastrochaena* (arrow) shells in their borings. Calcareous lining (CL) of *Lithophaga* aperture is clearly visible. Slab of the Op_1 hardground — Góra Kluczowa 2.

Plate 4

Organic structures characteristic for the second and the third links of the order of succession, i.e. belonging to the later colonizers and late successional dominants associations.

1a. *Trypanites* boring — morphotype I (= *Trypanites weisei*). Note undulose course of boring channel (arrow). Slab of the hardground — Występy.

1*b*. Different *Trypanites* borings — morphotype I (= *Trypanites weisei*). Note straight course of boring channels. Slab of the MO$_3$ hardground — Występy.
1*c*. Similar to 1*b* *Trypanites* borings — morphotype I (= *Trypanites weisei*). Slab of the MO$_3$ hardground — Występy.
2. *Trypanites* borings — morphotype II. Short boring channels resembling those of Recent *Polydora* is visible (arrow). Slab of the M$_3$ hardground — Góra Skorkowska.
3. Single borings — morphotype I. Short, straight boring channel with drop-like ending. Note thin cementation aureoles (CA) around bioturbation structures. Slab of the M_{MO_3} hardground — Góra Bukowa.
4. Single borings — morphotype II. Long, straight channel with tapered ending is similar to those of Recent Sipunculida. Slab of the Og$_3$ hardground — Głuchowiec.

Plate 5

Organisms and organic structures characteristic for the second and the third link of the order of succession.

1. Single borings — morphotype II. Long, slightly undulated chisel- ended channel amaizingly resembles those of Recent Stipunculida. Slab of the Og$_4$ hardground — Góra Kościółek.
2. Single borings — morphotype III. This boring — narrow channel with bell-like ending (arrow) is similar to those of Recent Echinoidea. Slab of the M$_6$ hardground — Brzegi.
3*a*. Remnants of oyster shells attached to the hardground surface. Shell of oyster which colonised firm ground and sank a little in bottom deposit is marked by solid (black) arrow. Shell of oyster which attached to hardground and spreaded out over the surface is denoted by another arrow. Therefore the first oyster belong to the later colonizers and the latter to the late successional dominants association. Slab of the Og$_3$ hardground — Góra Kościółek.
3*b*. Cross-section of the *Liostrea* shell sunk a little in the bottom sediment points out the stage of firm ground. This *Liostrea* belongs to the later colonizers association. Slab of the Op$_1$ hardground — Góra Kluczowa 2.
4. Numerous specimens of *Cycloserpula* resembling specimens of *Flucticularia* Regenhardt, 1961 (Ware 1975) are visible. They are attached to walls of hardground crevice. Slab of the M$_3$ hardground — Występy.

Plate 6

Early diagenetic cements induced by biota preserved either as the traces or skeletal remains within hardground formations.

1. Rigid micrite is visible within thin cementation aureole around single boring — morphotype II (BS). Stained (with A.R.S. + P.F.) peel. Slab of the Og$_4$ hardground — Góra Kościółek.
2*a*. Thick cementation aureole (arrow) is developed around *Thalassinoides paradoxicus* (Tp) burrow. Slab of the M$_3$ hardground — Występy.
2*b*. Thick cementation aureole is developed around *Thalassinoides paradoxicus* burrow (left arrow) and bivalve burrows (central arrow). Slab of the MO$_4$ hardground — Góra Kościółek.

3. Rigid micrite representing thick aureole, enriched in Fe and brown opaque material, is developed around undefined burrow (B). This micrite is darker than that in 1. Stained (with A.R.S. + P. F.) peel. Slab of the Ow hardground — Góra Kluczowa 2.
4. Patchy micrite (arrows) is developed within fragment of branching coral colony of *Calamophylliopsis*. Slab of the M_6 hardground — Brzegi.

Plate 7

Early diagenetic cements induced by biota maintained either as the traces or skeletal remains within hardground formations.

1. Patchy micrite in a form of irregular fungus attached to the surface of *Isastrea* colony is clearly visible. Slab of the Pl_2 hardground — Góra Skorkowska.
2. Small irregular patches (arrows) represent patchy micrite. These patches may envelope skeletal remains (left arrow). Slab of the M_6 hardground — Brzegi.
3. One of the strange structures within rigid micrite. In author's opinion these are remnants of organic-algae tubes filled up with calcite. SEM image of etched, polished surface of a rock chip. Magnification about 700×. Slab of the Op_1 hardground — Góra Kluczowa 2.

4*a*. Chain of pellet-like micrite aggregates (arrows) between sediment grains (ooids) is clearly visible. Stained (with A.R.S. + P.F.) thin section. Crossed nicols. Slab of the Op_1 — Góra Kluczowa 2.

4*b*. Chain of pellet-like micrite aggregates (arrows) is hardly visible compared with that in 4a. Unstained peel. Slab of the Op_1 hardground — Góra Kluczowa 2.

5*a*. Enlarged view of 5b. Rigid micrite is visible around the fragment of sparite inclusion. Stained (with A.R.S. + P.F.) thin section. Parallel nicols. Slab of the Pl_3 hardground — Góra Bukowa.

5*b*. Sparite inclusion is enveloped by rigid micrite (arrows). Stained (with A.R.S. + P.F.) thin section. Parallel nicols. Slab of the Pl_3 hardground — Góra Bukowa.

Plate 8

Other early diagenetic cements identified within hardground formations.

1. Coarse fringes are developed around rather large sedimentary grains. Note thickness of fringes and the habit of each crystals within fringes. Unstained acetate peel. Slab of the Ca hardground — Góra Kluczowa 1.
2. Asymmetrical fringe is situated on lower surface of skeletal remain (bivalve shell). Note crystals stacked on each other within the fringe and calcite sparite mosaic replacive after aragonite skeletal fabric. Stained (with A.R.S. + P.F.) acetate peel. Slab of the Ca hardground — Góra Kluczowa 1.

3*a*. Asymmetrical fringes resembling the "gravitational" cement by Müller (1971) are situated on underside surface of three grains. Stained (with A.R.S. + P.F.) thin section. Parallel nicols. Slab of the Ca hardground — Góra Kluczowa 1.

3*b*. Asymmetrical fringes resembling the "gravitational" cement by Müller (1971) are developed on underside surface of grains and corrosion residuum within *Thalassinoides paradoxicus* burrows. Unstained thin section. Parallel nicols. Slab of the M_3 hardground — Góra Skorkowska.

4. Acicular/bladed fringes are developed around three ooids. Note acute shingle-like endings of many crystals within fringes. Note also acicular crystals and needle-

like inclusions within some crystals. Stained (with A.R.S. + P.F.) acetate peel. Slab of the Og_3 hardground — Góra Kościółek.

5. Enlarged view of acicular/bladed fringe. Note irregular faces of each crystals (arrows) and acute shingle-like ending of one of them. SEM image of fractured surface of a rock chip. Slab of the Og_3 hardground — Góra Kościółek.
6. Enlarged view of acicular/bladed fringe which is situated on ooid (G) surface. Acute shingle-like endings (arrows) of each crystals are clearly visible. Note an acicular crystal (left arrow). SEM image of fractured surface of a rock chip. Slab of the Og_3 hardground — Góra Kościółek.

Plate 9

Other early diagenetic cements identified within hardground formations.

1. Acicular/bladed fringes are developed in a form of a "palisade" cement resembling that found in Recent sediments (cf. Schroeder 1973). This "palisade" cement fills up the ostracod valves. Unstained acetate peel. Slab of the Pl_1 hardground — Góra Kluczowa 1.

2*a*. Acicular/bladed fringe is developed on the surface of small ooid. This fringe is consisted of fibre crystals. Unstained acetate peel. Slab of the FO_1 hardground — Występy.

2*b*. Enlarged view of acicular/bladed fringe which is consisted of fibre crystals. Acicular cement crystals in conjunction with radial elements of ooid (arrow) are clearly visible. SEM image of polished and etched surface of a rock chip. Slab of the FO_1 hardground — Występy.

3*a*. Microcrystalline fringe around micro-ooid grain (black arrow) is consisted of tiny, acicular crystallites. Note calcite overgrowth on echinoderm fragment (another arrow). Unstained acetate peel. Slab of the MO_4 hardground — Góra Kościółek.

3b. Enlarged view of two or three microcrystalline fringes around pellet grains. Note composite structure of these fringes. SEM image of polished and etched surface of a rock chip. Slab of the Pl_1 hardground — Góra Kluczowa 1.

3*c*. Enlarged view of microcrystalline fringe around pellet grain (G) shows two layers of tiny acicular crystallites built up the fringe. SEM image of polished and etched surface of a rock chip. Slab of the Pl_1 hardground — Góra Kluczowa 1.

4. Acicular/bladed fringe is consisted of tiny crystals hardly visible on microooid surface. Unstained acetate peel. Slab of the MO_1 hardground — Występy.

Plate 10

Other early diagenetic cements identified within hardground formations.

1*a*. Isometric fringe is developed around small ooid grain. Note irregular shape of this grain and thickness of the fringe. Stained (with A.R.S. + P.F.) acetate peel. Slab of the Og_3 hardground — Góra Kościółek.

1*b*. Enlarged fragment of isometric fringe. Note irregular, unclear boundary between grain and the fringe in comparison with ooid and acicular/bladed fringe on its right. Note also amoeboid (neomorphic) intercrystalline boundaries within the fringe. Stained (with A.R.S. + P.F.) acetate peel. Slab of the Og_3 hardground — Góra Kościółek.

1c. Enlarged view of the isometric fringe. Clear relationship between the fringe of enormous thickness and relic of the grain in its center emphasises neomorphic character of isometric fringes. Stained (with A.R.S. + P.F.) acetate peel. Slab of the Og$_3$ hardground — Góra Kościółek.

2. Micrite fringes are developed around two ooids. These fringes can be easily distinguished (arrows) from adjacent micrite. Stained (with A.R.S. + P.F.) thin section. Crossed nicols. Slab of the Ow hardground — Góra Kluczowa 2.

3a. Micrite cement occurs as a pellet-like aggregates within oolite deposit. This cement represents friable micrite. Stained (with A.R.S. + P.F.) thin section. Crossed nicols. Slab of the Op$_1$ hardground — Góra Kluczowa 2.

3b. Single pellet-like aggregates are joined together in larger micrite sphaeres. This is the initial stage in shaping of rigid micrite. Stained (with A.R.S. + P.F.) acetate peel. Slab of the Og$_6$ hardground — Sobków.

4. This is a particular mode of micrite cement occurrence within oolite deposit. The mode of ooids binding is peculiar to vadose cement. Sparite (S) fills up remaining pore spaces. Stained (with A.R.S. + P.F.) acetate peel. Slab of the Og$_6$ hardground — Sobków.

Plate 11

Other early diagenetic cements occurred within hardground formations.

1. Pellet-like micrite aggregates as pendant and pimple-like structures on ooids' surfaces. Note central hole (microalgae tube?) representing nucleus (arrow) in one of the pellet-like micrite aggregates. Stained (with A.R.S. + P.F.) thin section. Crossed nicols. Slab of the Op$_1$ hardground — Góra Kluczowa 2.

2. Pore space between three ooids (arrows) is completely filled up with rigid micrite cement. Note barely distinctive outline of these ooids. Unstained acetate peel. Slab of the Ow hardground — Góra Kluczowa 2.

3. Single pellet-like aggregates are easily detected within rather loose micrite cement. Note peculiar objects as the nuclei (arrows) of some pellet-like aggregates. SEM image of polished and etched surface of a rock chip. Slab of the Op$_1$ hardground — Góra Kluczowa 2.

4. Individualised pellet-like aggregate within rigid micrite cement. Note outer, coarse crystalline rim outlined fine crystalline center. SEM image of polished and etched surface of a rock chip. Slab of the Op$_1$ hardground — Góra Kluczowa.

5a. Enlarged view of rigid micrite cement. Single pellet-like aggregates are, in most, indistinctive. It is conceivable to imagine one of them (arrows). SEM image of fractured surface of a rock chip. Slab of the M$_3$ hardground — Góra Kościółek.

5b. Basic units (arrows) of the micrite architecture. They are consisted of 5—7 crystals in a form of flowers. SEM image of fractured surface of a rock chip. Slab of the M$_3$ hardground — Góra Kościółek.

Plate 12

Other early diagenetic cements occurred within hardground formations.

1a. Microsparite is developed on grains surfaces as meniscus structures (arrow). The remaining pore space are filled up with sparite. Unstained acetate peel. Slab of the Ca hardground — Góra Kościółek.

1*b*. Meniscus outline of microsparite cement binding the adjacent grains together. Remaining, central pore is filled up with sparite. Stained (with A.R.S. + P.F.) acetate peel. Slab of the FO_1 hardground — Występy.

1*c*. Pore spaces within pelletal deposit are completely filled with microsparite cement mosaic. Note relics of acicular/bladed fringes on some deposit grains. Unstained acetate peel. Slab of the Pl_1 hardground — Góra Kluczowa 1.

2. Skeletal (bivalve) remain laying on the hardground surface is filled with sparite mosaic. This sparite is cut by bivalve "X" and subsequently by *Trypanites weisei*. Slab of the Og_6 hardground — Sobków. Magnification c.a. ×1,5.

3*a*. Quartz/chalcedony (Q) crystal occurs within sparite mosaic. The position of this crystal points out the three visible diagenetic events. The first s precipitation of acicular/bladed fringes around ooids, the second is precipitation of sparite and the third is replacement of calcite sparite by quartz. Unstained acetate peel. Slab of the FO_1 hardground — Występy.

3*b*. Both of sediment grains and calcite sparite (S) are destroyed by large quartz/chalcedony (Q) crystal. Stained (with A.R.S. + P.F.) acetate peel. Slab of the FO_2 hardground — Góra Bukowa.

3*c*. Silica relic (Qr) within calcite sparite crystal. Note irregular boundary of this calcite crystal. Silica relic points out the presence of quartz-calcite replacement. Stained (with A.R.S. + P.F.) thin section. Nicols parallel. Slab of the M_6 hardground — Brzegi.

Plate 13

Polarization of the fauna within some hardground formations.

1. General view of *Thalassinoides paradoxicus* (Tp) burrows within hardground formation. Note laminated structures encrusted top of burrows, and borings pointed out colonization of burrow walls by bivalves. Slab of the M_3 hardground — Góra Bukowa.

2*a*. Slightly enlarged view of *Thalassinoides paradoxicus* burrows cross-section. Laminated structures encrusted top of these burrows are cut by bivalve borings in a distinct manner pointing out cementation of the laminated structures in statu nascendi. Note other bivalve borings penetrating hardground surface. Slab of the M_3 hardground — Góra Bukowa.

2*b*. Laminated structures (arrows) in a form of piles resembling stromatolites encrust walls of *Thalassinoides paradoxicus* burrows just beneath hardground surface. Slab of the M_3 hardground — Występy.

Plate 14

Effects of neomorphic processes observed within hardground formations.

1. Large pseudosparite (PS) crystal is exploded within calcite mosaic. Pseudosparite crystal also destroyes fine sedimentary grains. Unstained thin section. Nicols parallel. Slab of the MO_1 hardground — Występy.
2. Pseudosparite crystals (arrow) destroy original ooid structure. Stained (with A.R.S. + P.F.) acetate peel. Slab of the FO_1 hardground — Występy.
3. Result of recrystallization within micrite (aggrading neomorphism *sensu* Folk 1965). Amoeboid crystals of neomorphic microsparite form centres of circles

enveloped by fine crystalline rim. Stained (with A.R.S. + P.F.) acetate peel. Slab of the M_8 hardground — Sobków.

4*a*. Acicular/bladed fringe developed on one ooid (arrow) is partly replaced by micrite (m). Acicular/bladed fringe situated on another (upper) ooid remains unaltered and the third fringe (on the lower ooid) is completely replaced by micrite (m). Remaining pore space is filled up with sparite (S). Stained (with A.R.S. + P.F.) thin section. Crossed nicols. Slab of the Op_1 hardground — Góra Kluczowa 2.

4*b*. Relic of acicular/bladed fringe (arrow) is visible on the ooid surface. Remaining ooid surface is occupied by micrite (m). Note the different character of acicular/bladed fringe developed on the surface of another ooid (on the right). That fringe is identical with isometric ones. SEM image of polished and etched surface of a rock chip. Slab of the Og_3 hardground — Góra Kościółek.

5. Sparite (S) is suggested to be replacive after acicular/bladed fringes and now, this sparite mosaic is binding adjacent grain together. SEM image of fractured surface of a rock chip. Slab of the Og_3 hardground — Góra Kościółek.

Plate 15

Effects of meteoric diagenesis and calcite by quartz replacement.

1*a*. Outline of the Nerineid shell (arrow) is filled with the sediment identical with that filled *Thalassinoides paradoxicus* burrows (B). Slab of the M_3 hardground — Występy.

1*b*. Nerineid shell just beneath hardground surface is partly filled with sparite mosaic and the sediment identical with that filling up burrows within the hardground formation. Slab of the Pl_1 hardground — Góra Kluczowa 1.

1*c*. Nerineid shell partly filled with sparite (dark). Outline of Nerineid shell not filled with sparite vanishes. Negative print of unstained acetate peel. Slab of the Pl_1 hardground — Góra Kluczowa 1.

2*a*. Sedimentary grain is completely filled with the quartz/chalcedony crystals. Some of the crystals are visible (arrow). Stained (with A.R.S. + P.F.) thin section. Crossed nicols. Slab of the Ca hardground — Góra Kluczowa 1.

2b. Result of *in situ* replacement of calcite (C) by quartz/chalcedony (Q). Note two generations of quartz/chalcedony crystals and visible replacement front (arrow). Stained (with A.R.S. + P.F.) acetate peel. Slab of the Og_6 hardground — Sobków.

Plate 16

Effects of calcite by quartz/chalcedony replacement.

1. Quartz/chalcedony (Q) is replacive after calcite (C) along primary structural defects of shell remnant. Note relics of primary structure within quartz/chalcedony crystal. Stained (with A.R.S. + P.F.) acetate peel. Slab of the Og_6 hardground — Sobków.
2. Fragment of calcite (C) fringe encrusted void wall (empty bivalve shell) is burried and partly destroyed by chalcedony/quartz (Q) crystals. Note the habit of quartz/chalcedony crystals which were also growing free at the time of replacement. Stained (with A.R.S. + P.F.) acetate peel. Slab of the Og_6 hardground — Sobków.

3. Patches of quartz/chalcedony inside ooids and within micrite cement (arrows) are clearly visible. Stained (with A.R.S. + P.F.) thin section. Nicols parallel. Slab of the Og_1 hardground — Lipia Góra.
4. Quartz/chalcedony (arrows) crystals are situated within calcite sparite mosaic filling bivalve boring. Stained (with A.R.S. + P.F.) acetate peel. Slab of the MO_5 hardground — Sobków.
5. Calcite (C) sparite mosaic filling a bivalve boring is replaced by the quartz/chalcedony (Q) fringe encrusting walls of the boring. Stained (with A.R.S. + P.F.) acetate peel. Slab of the Op_1 hardground — Góra Kluczowa 2.

Plate 17

Examples of Og_3 (Kościółek hill) and Og_2 (Piekielnica hill) hardground formations analysis.

The analysis is pointing out three stages of hardgrounds eogenetic cementation: *1* initial cementation by fibrous aragonite fringes under oxidizing conditions (R — stain); *2* fibrous fringes dissolution and alteration by micrite patches or isometric-equant/bladed fringes under oxidizing conditions; *3* later cementation by calcite spar under reducing conditions (V — stain).

Plate 18

Examples of FO_1 (Występy) and FO_2 (Bukowa hill) hardground formation analysis.

The analysis is delineating at least two stages of hardground eogenetic cementation: *1* initial cementation by fibrous aragonite fringes under oxidizing conditions (R — stain); *2* later surficial corrosion of the hardground FO_1 (contact dissolution of grains) under reducing conditions (V — stain) and final cementation by calcite spar.

Plate 19

Examples of MO_1 (Występy) and MO_4 (Kościółek hill) hardground formations analysis.

The analysis is showing two stages of hardground eogenetic cementation under reducing conditions (V, B — stain): *1* micrite cementation around the *Thalassinoides* and bivalve burrows supported by calcite cementation in a form of overgrowths and bladed fringes within adjacent areas; *2* final cementation by calcite spar.

Plate 20

Example of V (variant) hardground formation analysis.

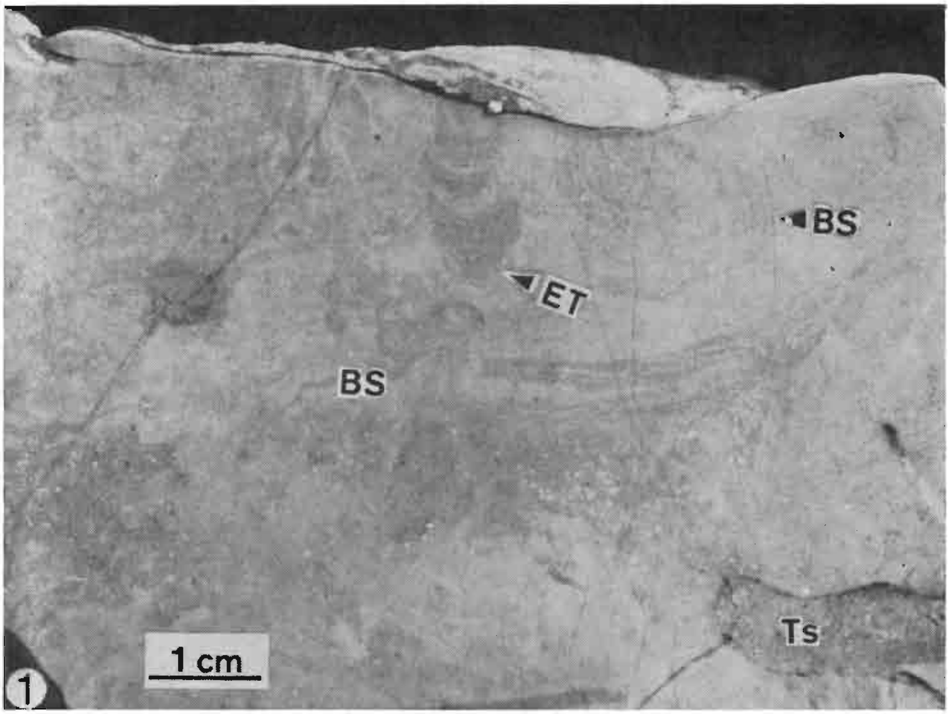
The analysis emphasises a change in cement type and also mineralogy at the span of 1 meter. Recognised cementation events were as follows: *1* initial cementation either by calcite micrite or aragonite fibrous fringes under oxidizing conditions

(R — stain); *2* final cementation by calcite spar and partial recrystallization of micrite under reducing conditions (V — stain).

Plate 21

Example of hardground M_3 analysis.*

The initial cementation is displayed by micrite either under oxidizing (R — stain) or reducing (V — stain) conditions. The final recrystallization of micrite might be more or less advanced.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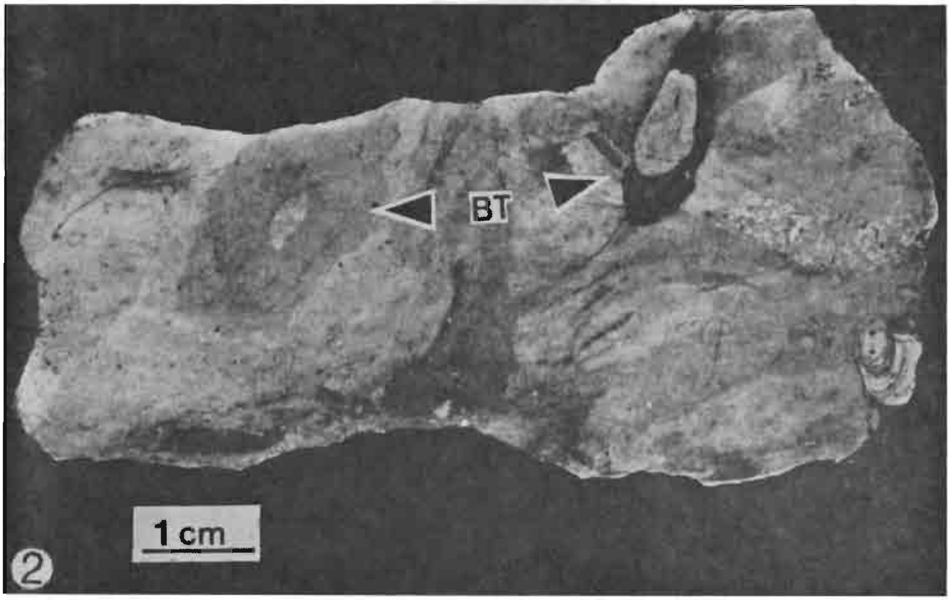
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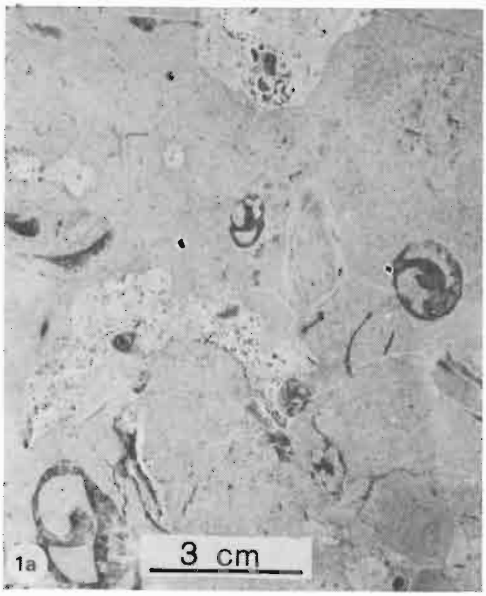
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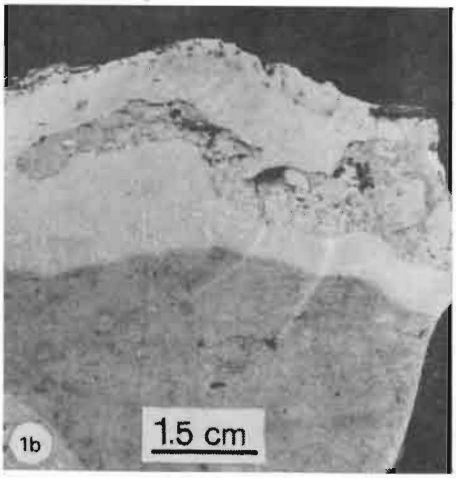
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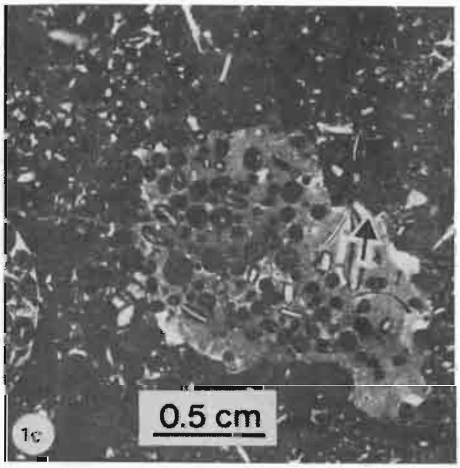
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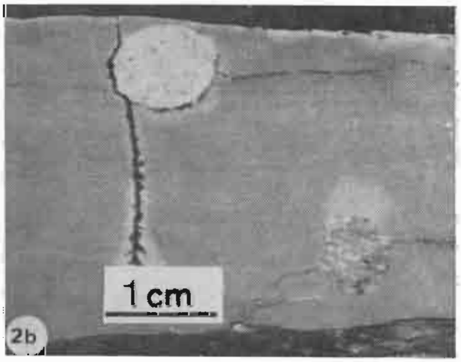
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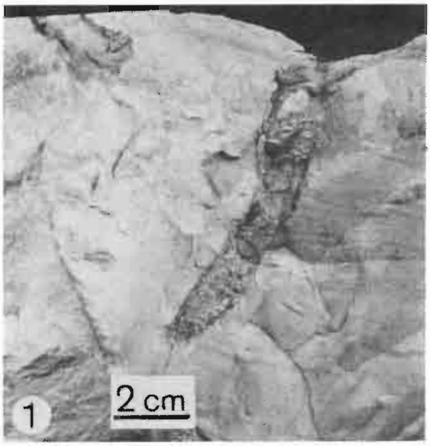
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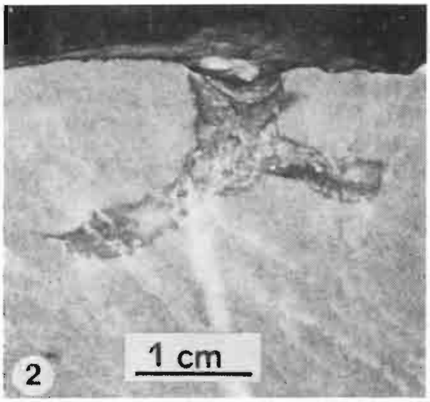
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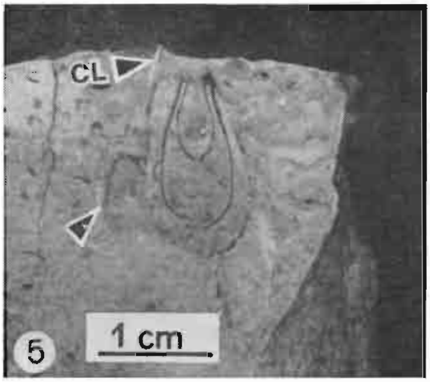
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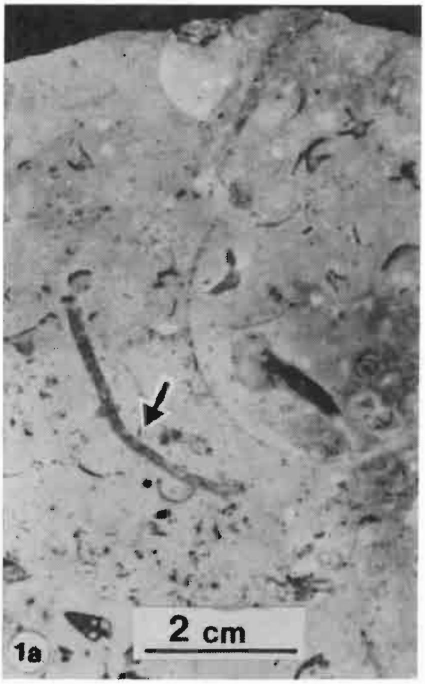
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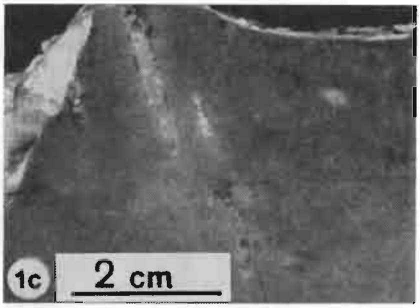
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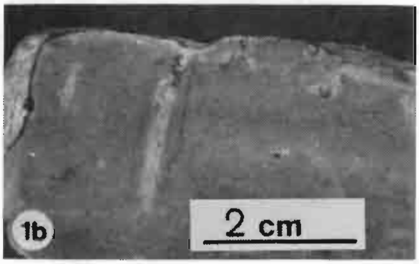
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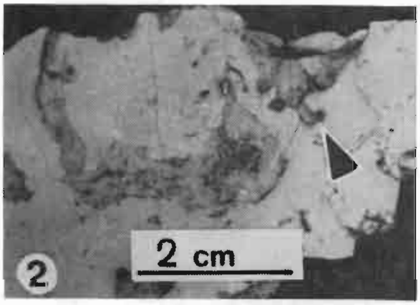
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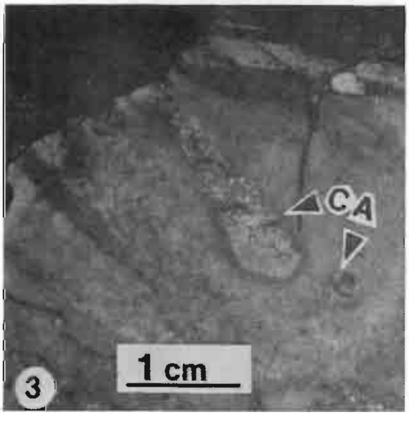
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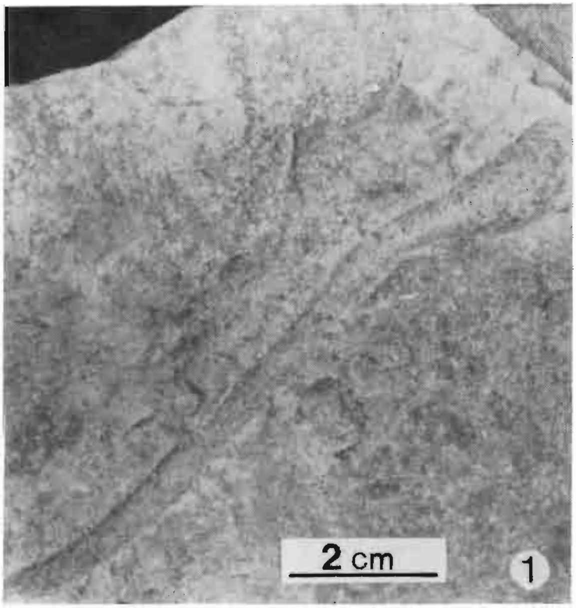
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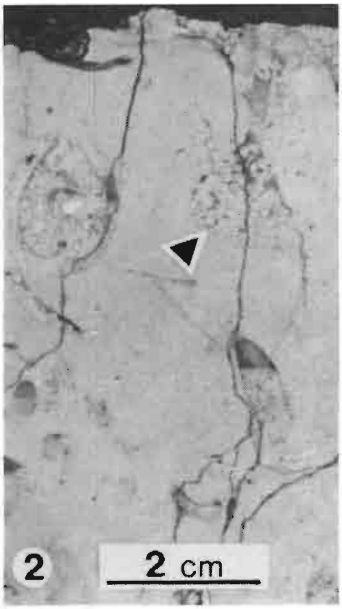
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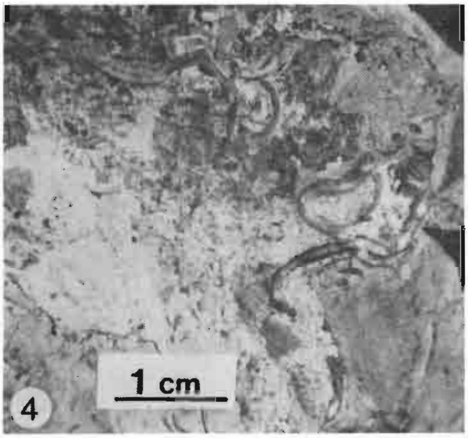
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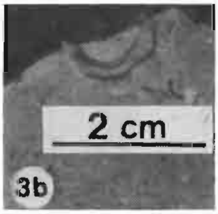
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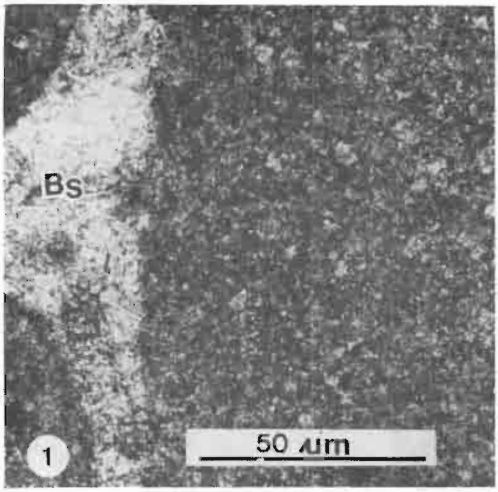
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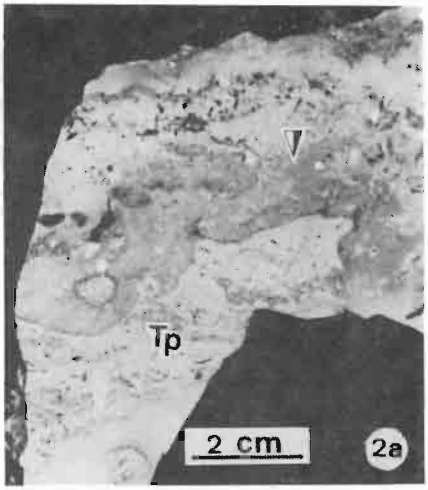
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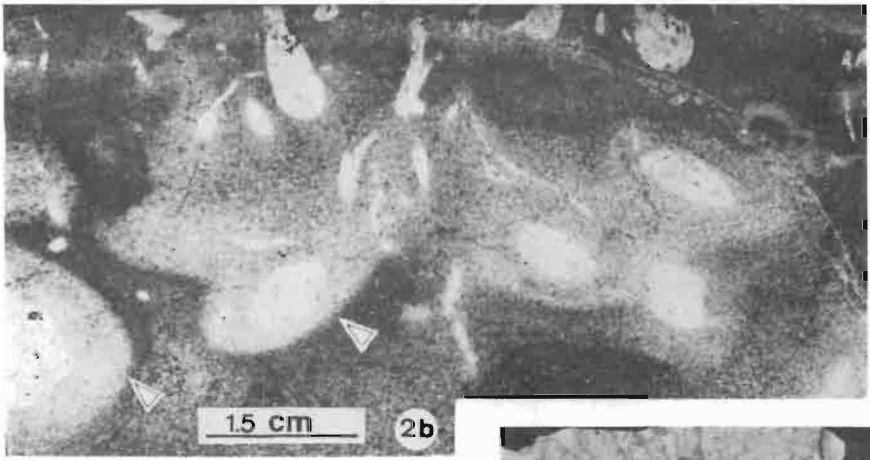
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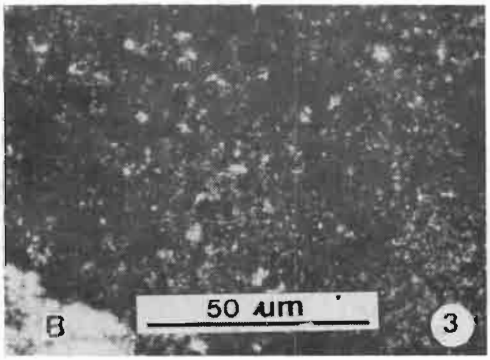
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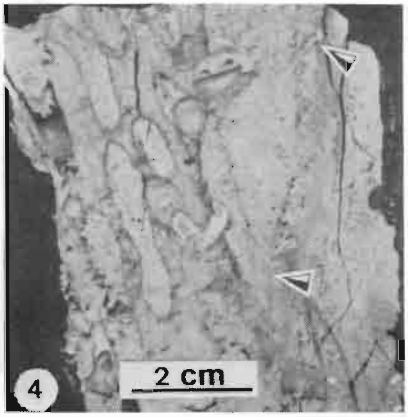
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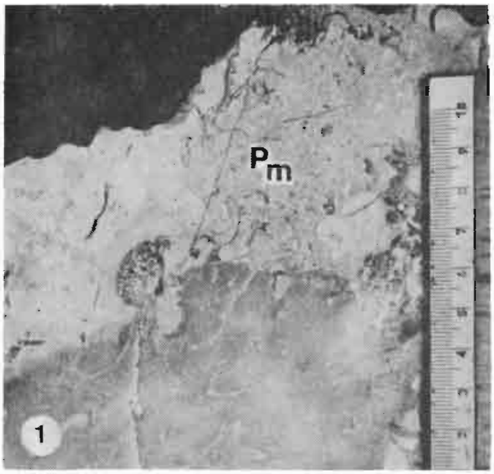
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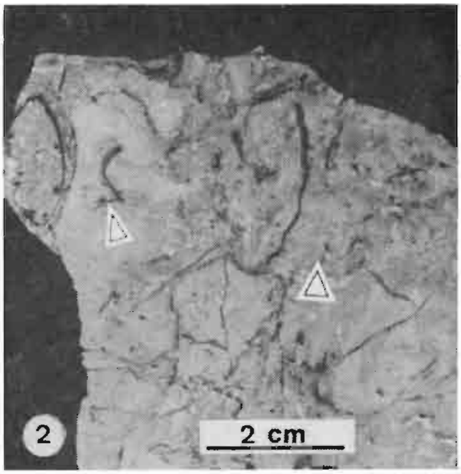
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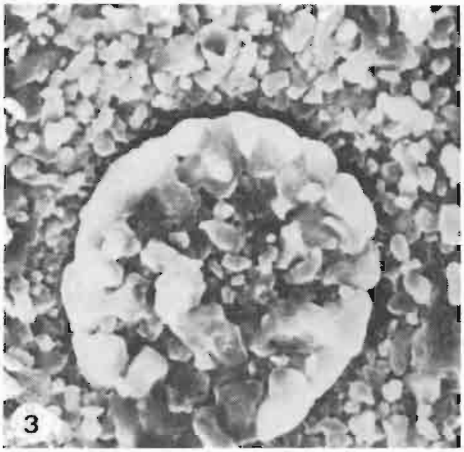
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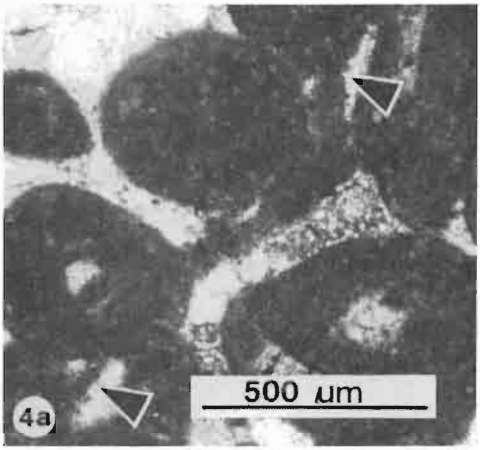
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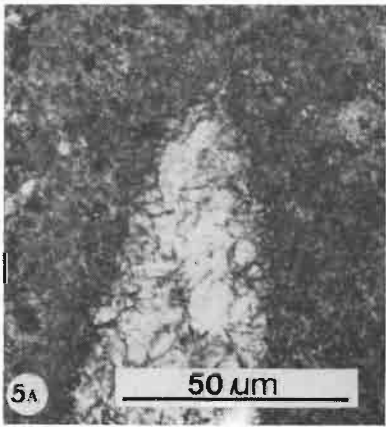
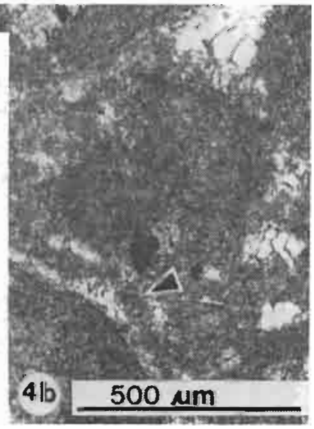

5A


5B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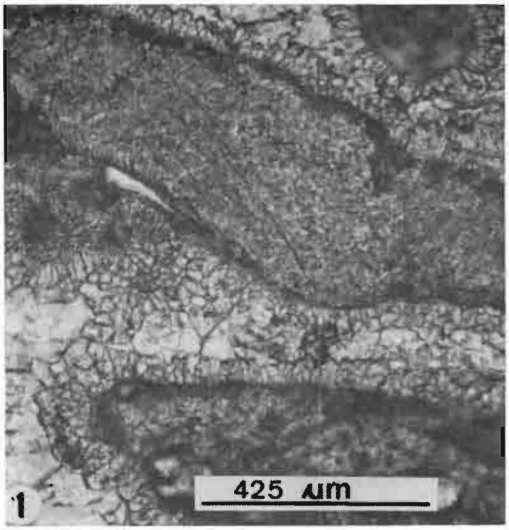
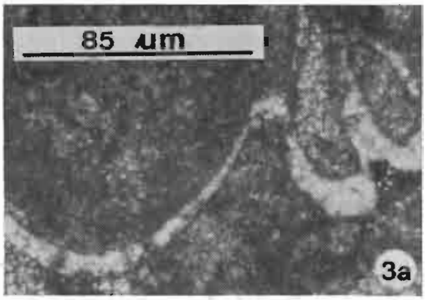

1
425 µm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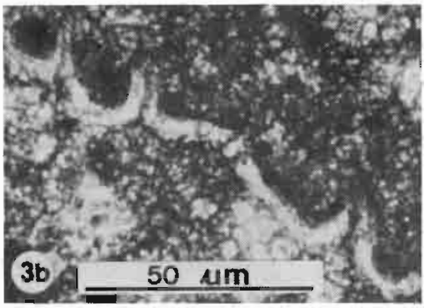
3a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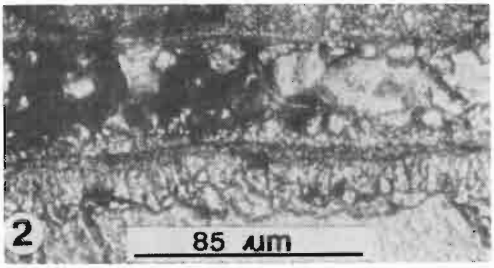
50 µm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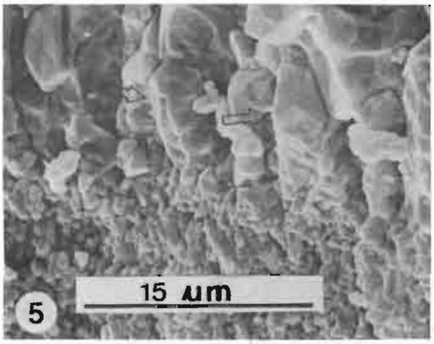
15 µm
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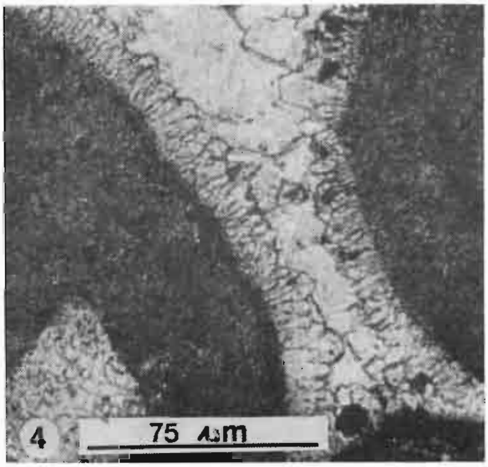
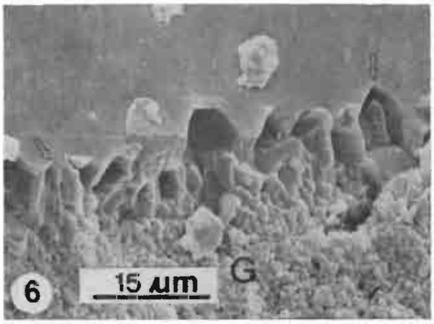
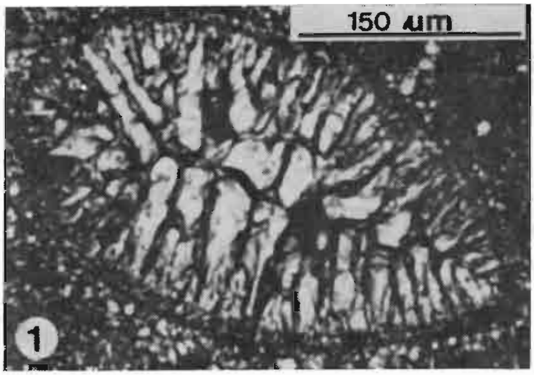
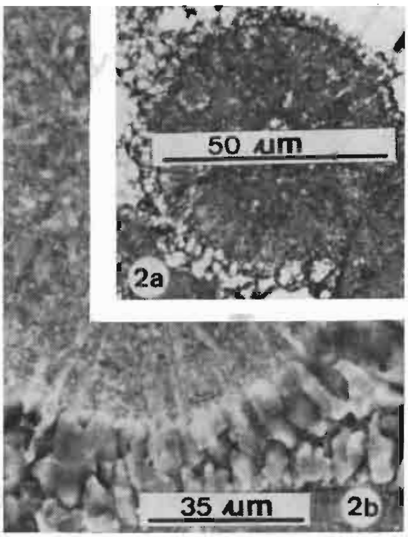
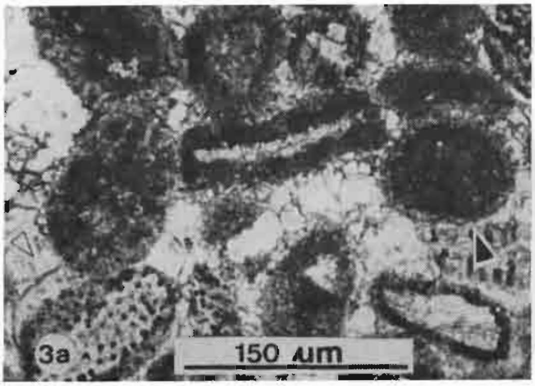

4
75 µm

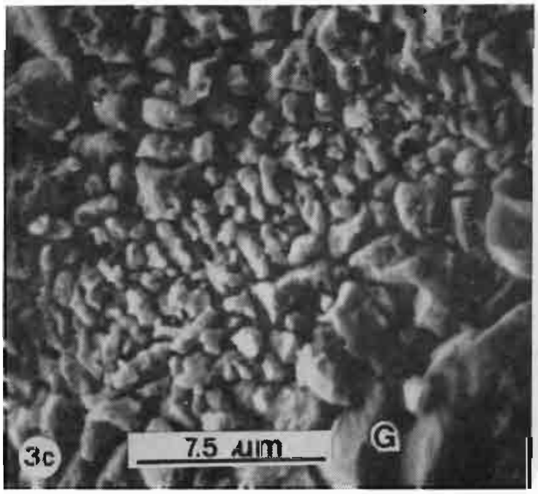

6
15 µm
G

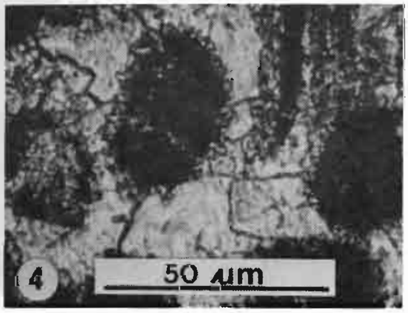

150 µm
1

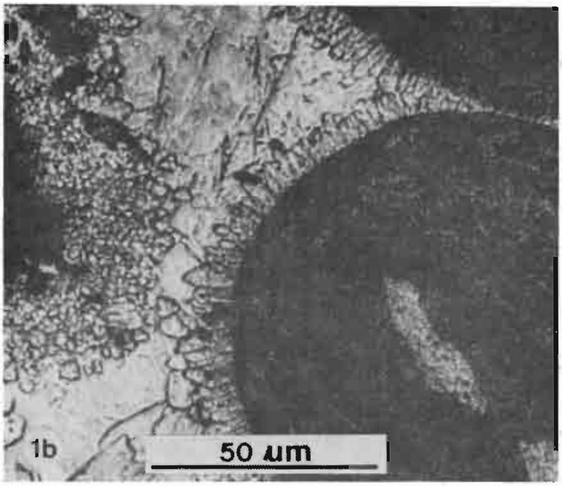

50 µm
2a
35 µm
2b


3a
150 µm


3b
25 µm


3c
7.5 µm
G


4
50 µm


1b
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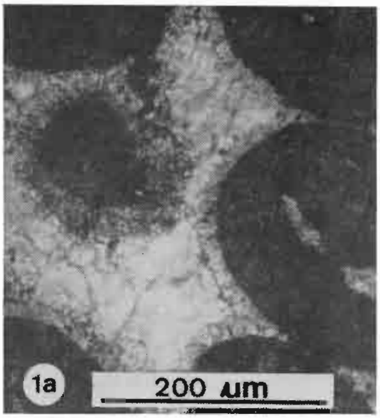
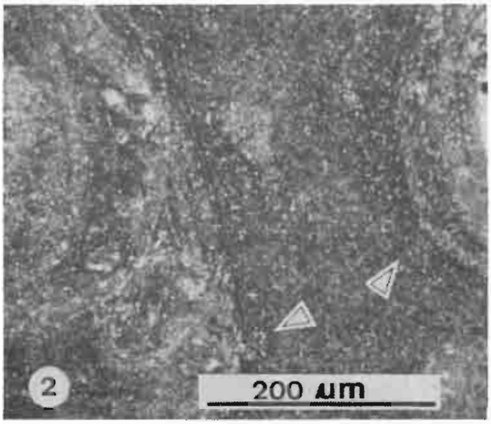

1a
200 µm


2
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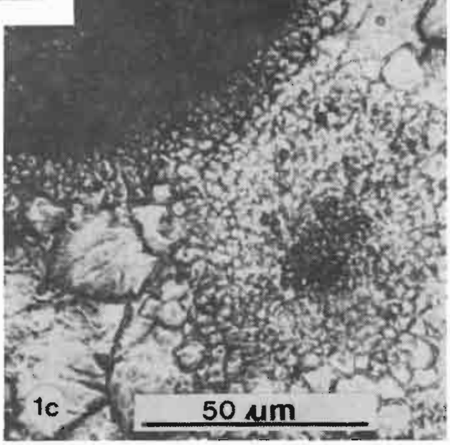
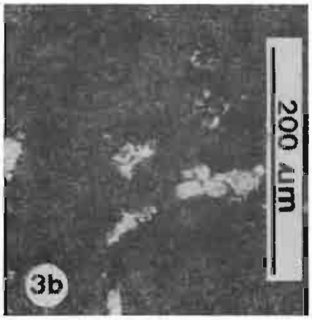
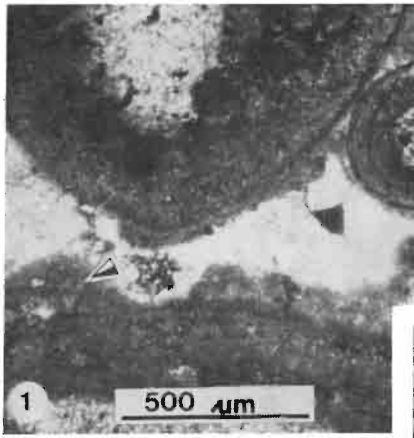
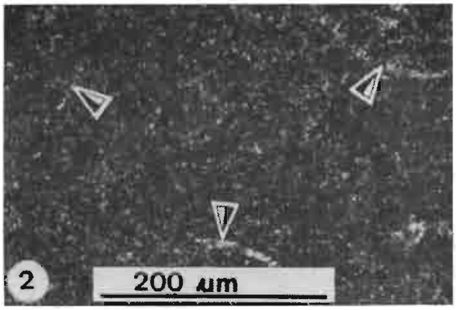

1c
50 µm

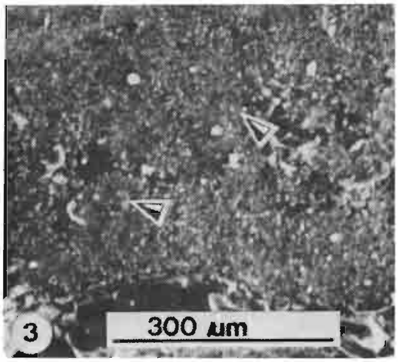

3a
400 µm

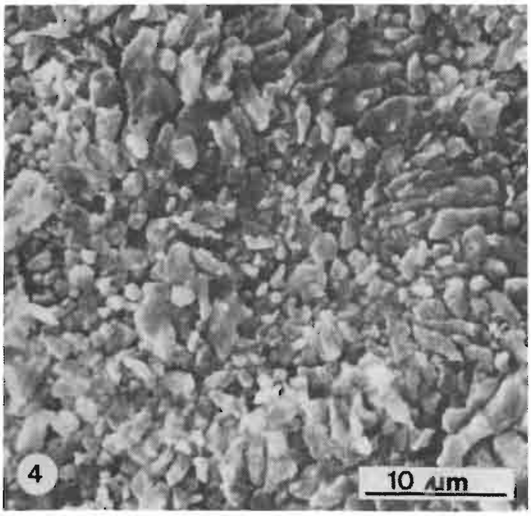

3b
200 µm

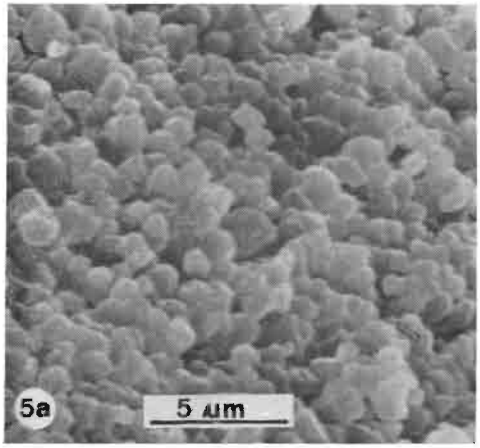

S
S
S
200 µm
4

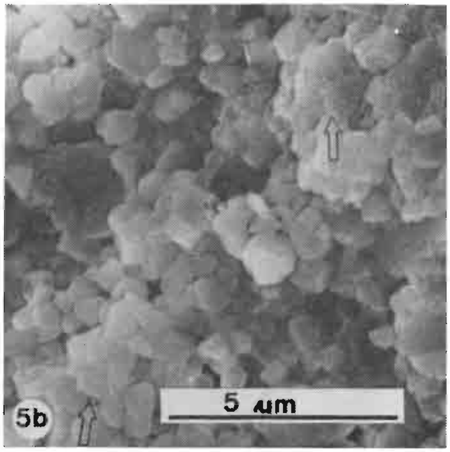

1
500 µm

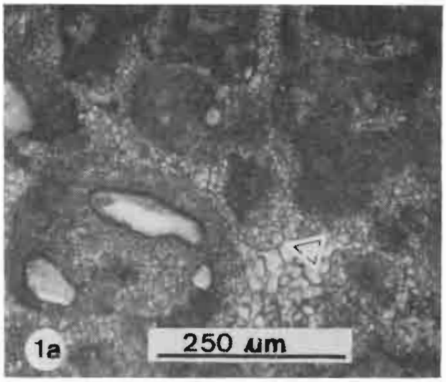

2
200 µm

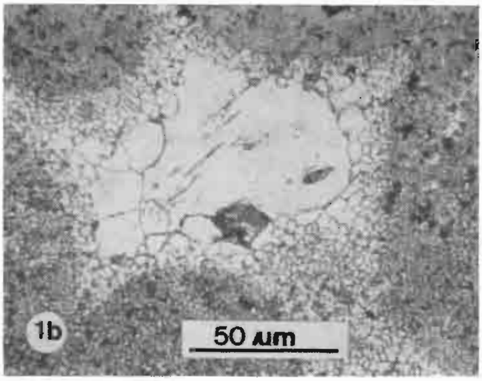

3
300 µm

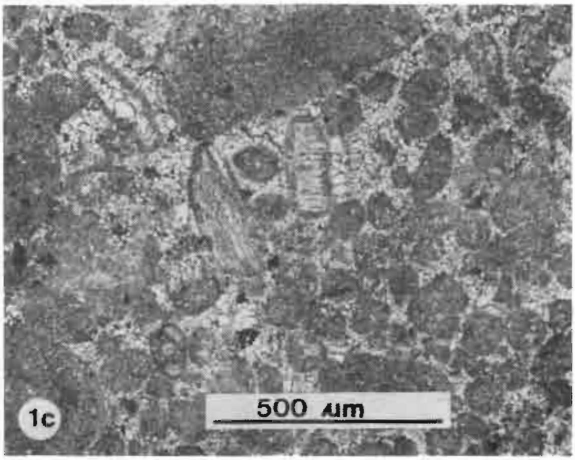

4
10 µm


5a
5 µm

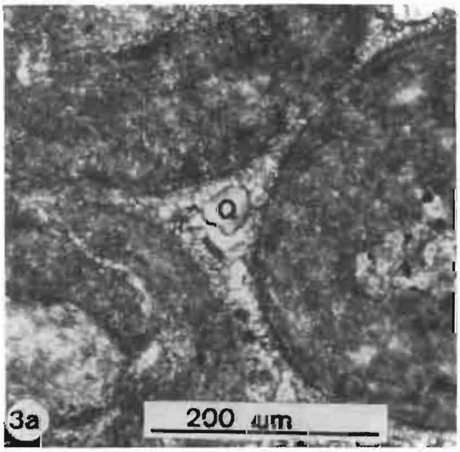

5b
5 µm

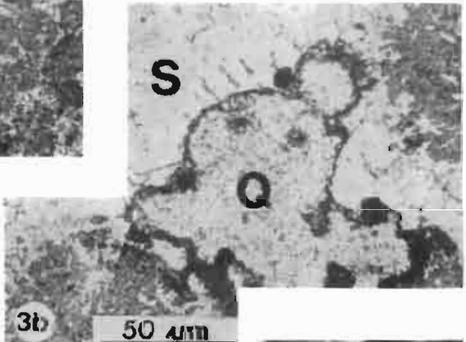

1a
250 µm

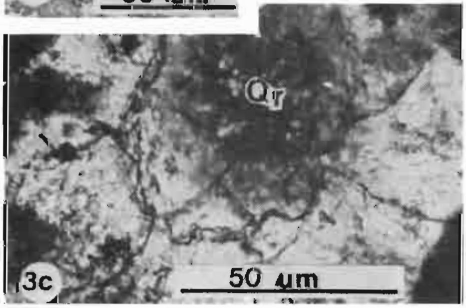

1b
50 µm

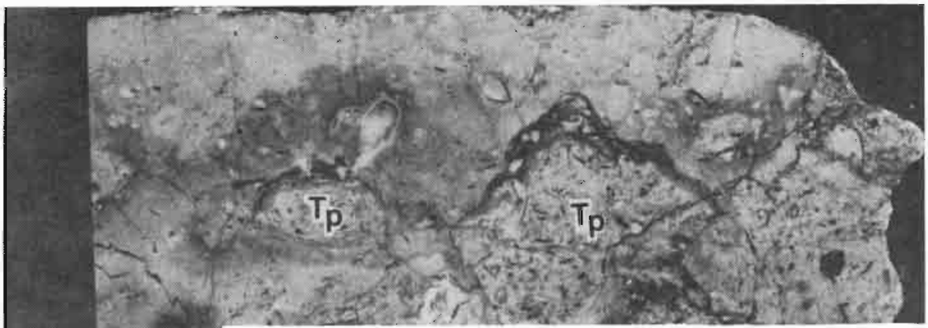

1c
500 µm

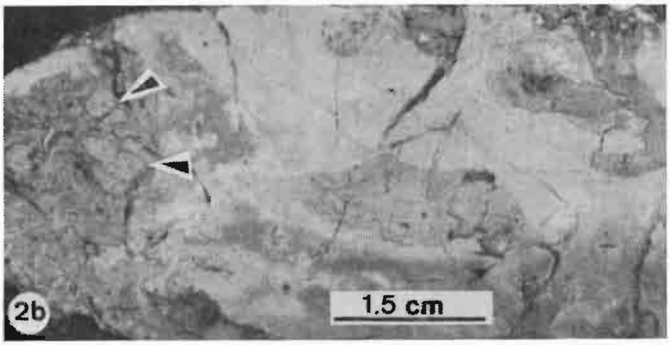

2

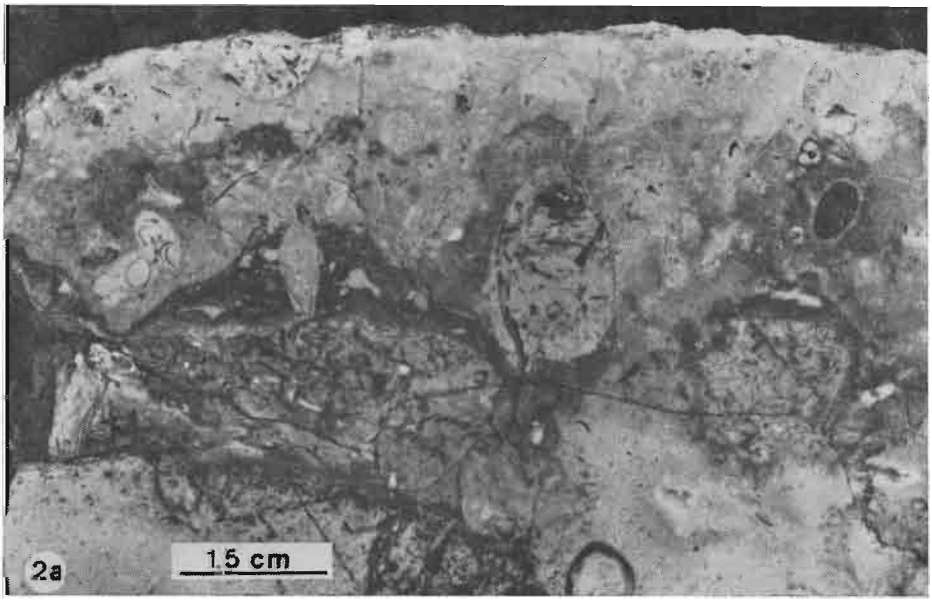

Q
3a
200 µm

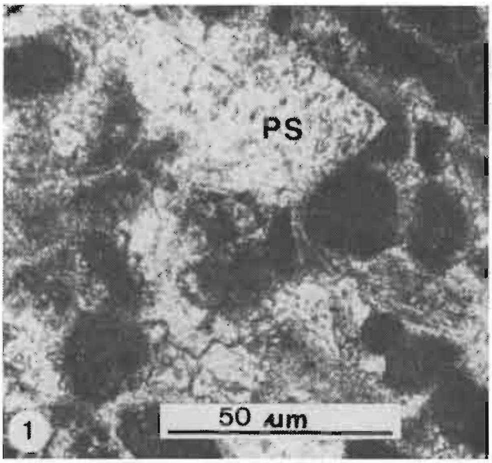

S
Q
3b
50 µm

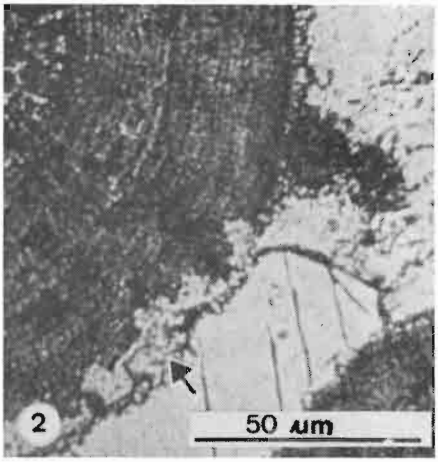

Qr
3c
50 µm

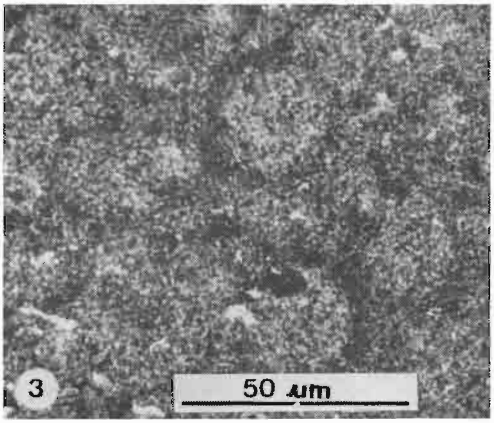

Tp
Tp
Tp
2 cm
1

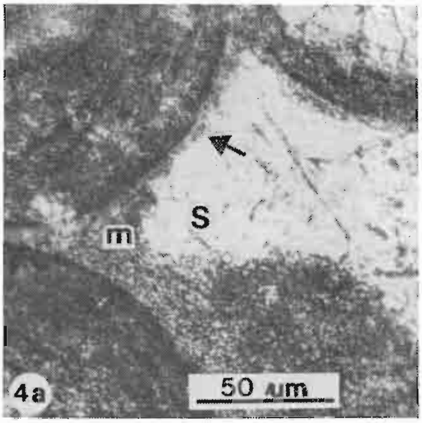

1.5 cm
2b

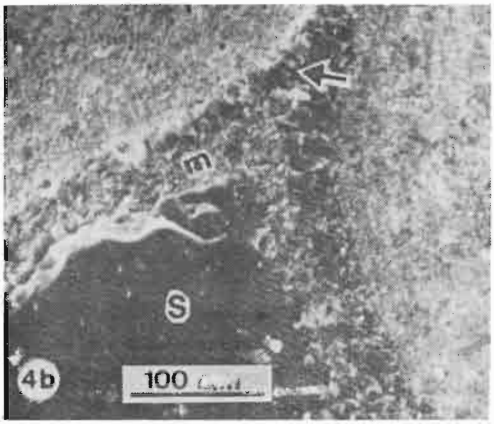

1.5 cm
2a

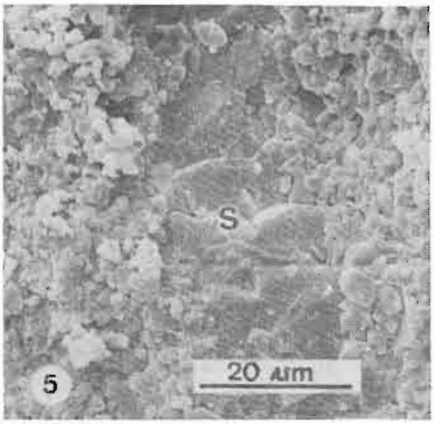

PS
50 µm
1


2
50 µm

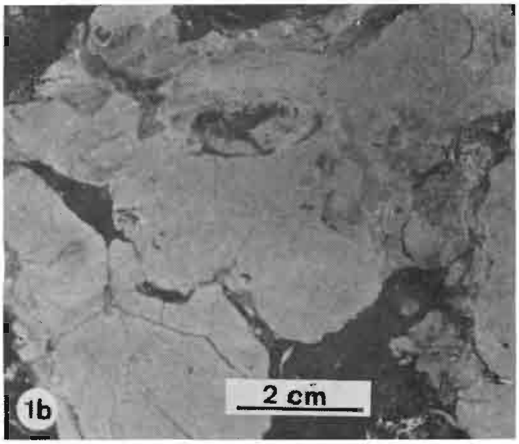

3
50 µm

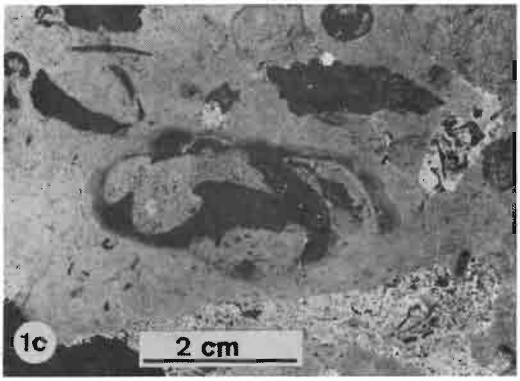

S
m
4a
50 µm

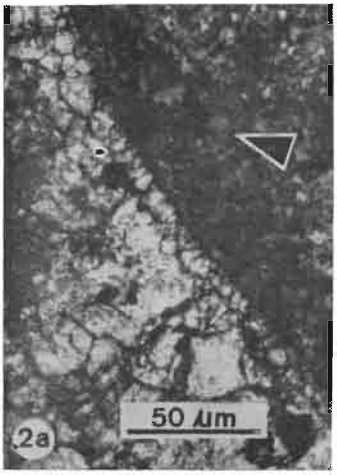

m
S
4b
100

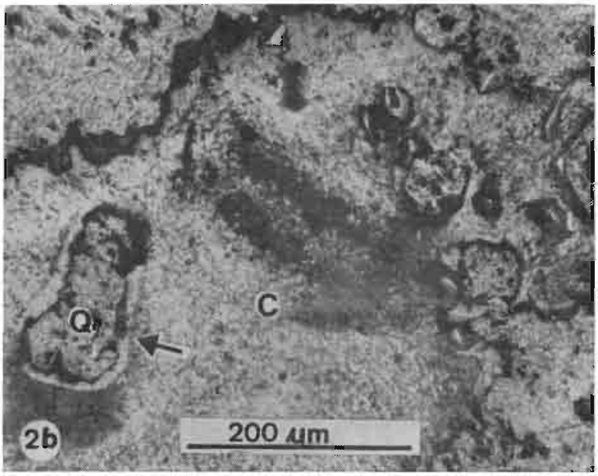

S
5
20 µm

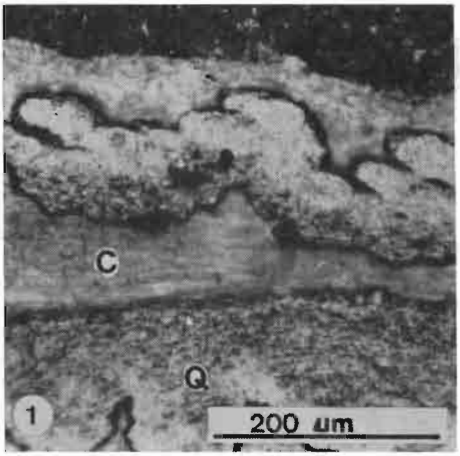

B
1.5 cm
1a

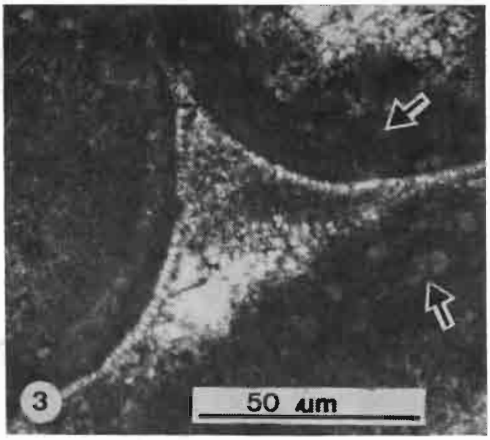

2 cm
1b

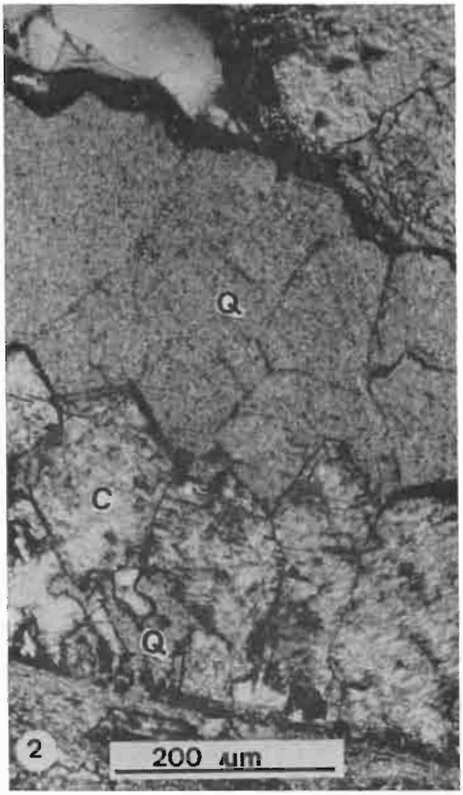

2 cm
1c

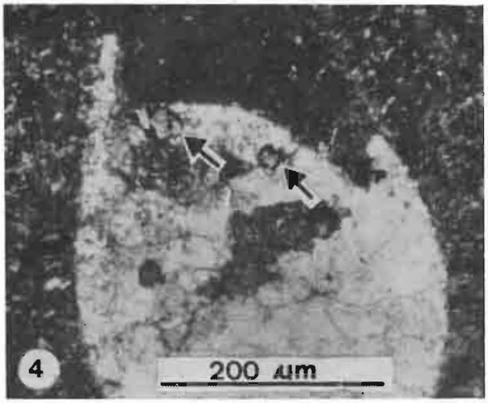

50 µm
2a

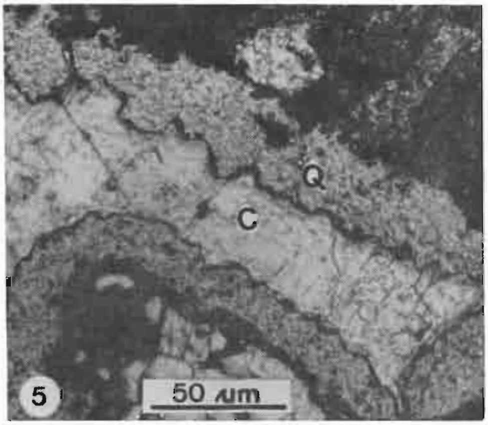

Q
C
200 µm
2b

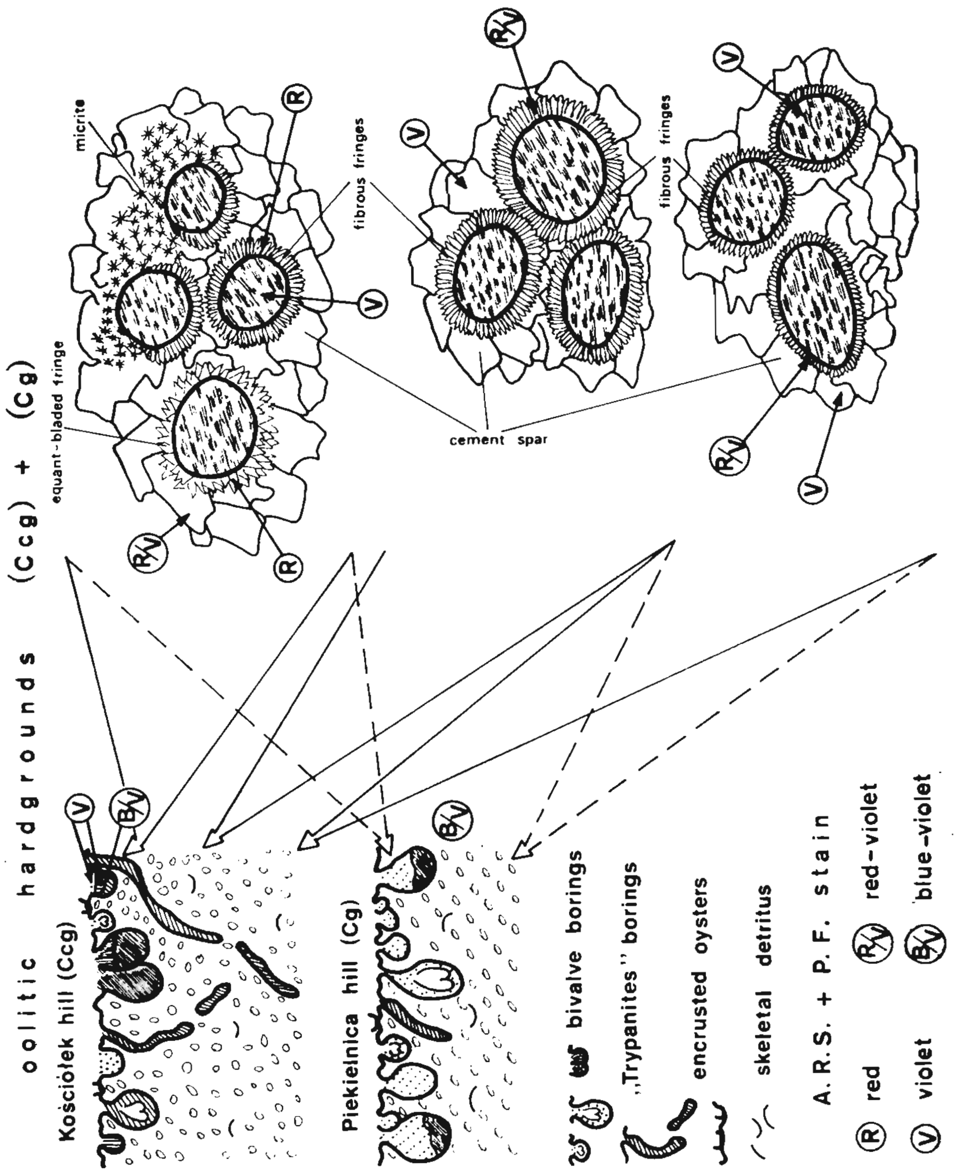

C
Q
1
200 µm


3
50 µm

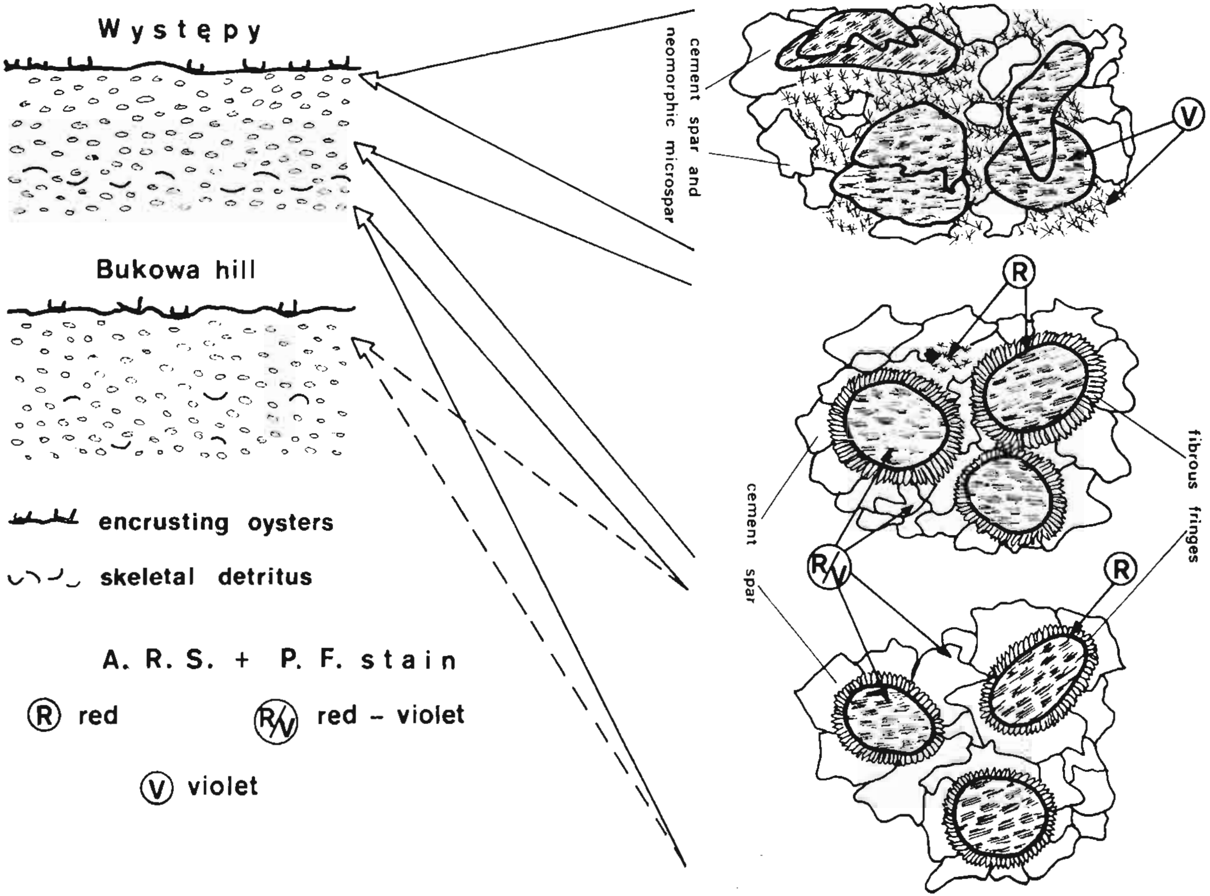

Q
C
Q
2
200 µm

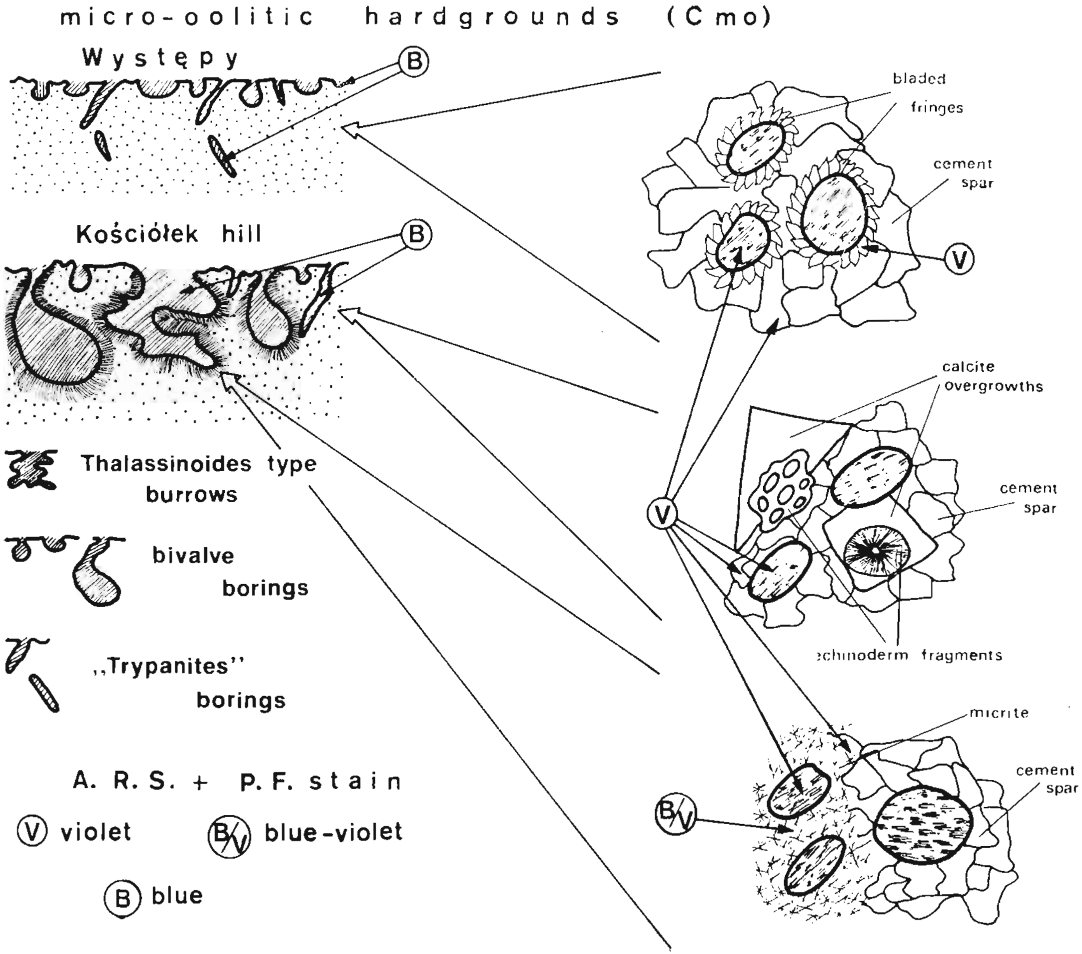

4
200 µm

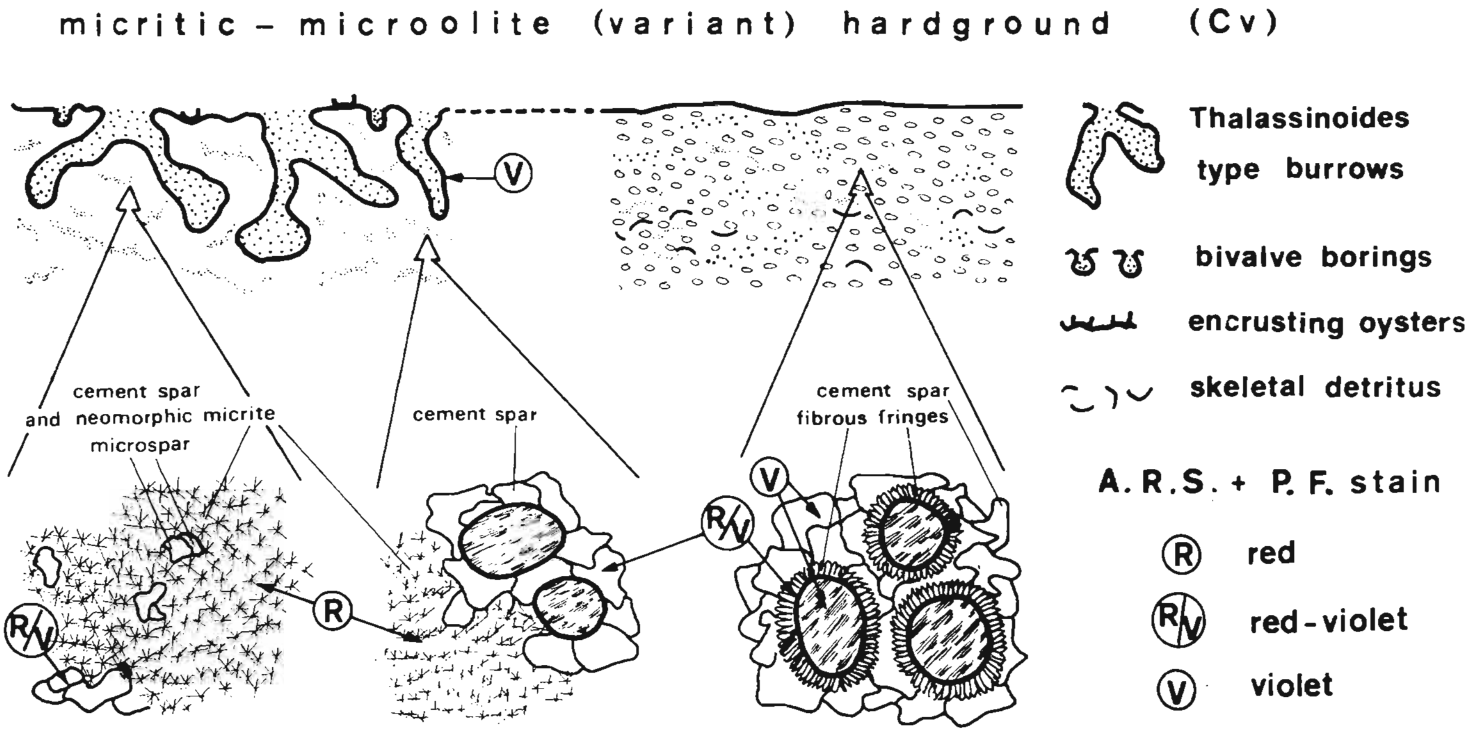

Q
C
5
50 µm

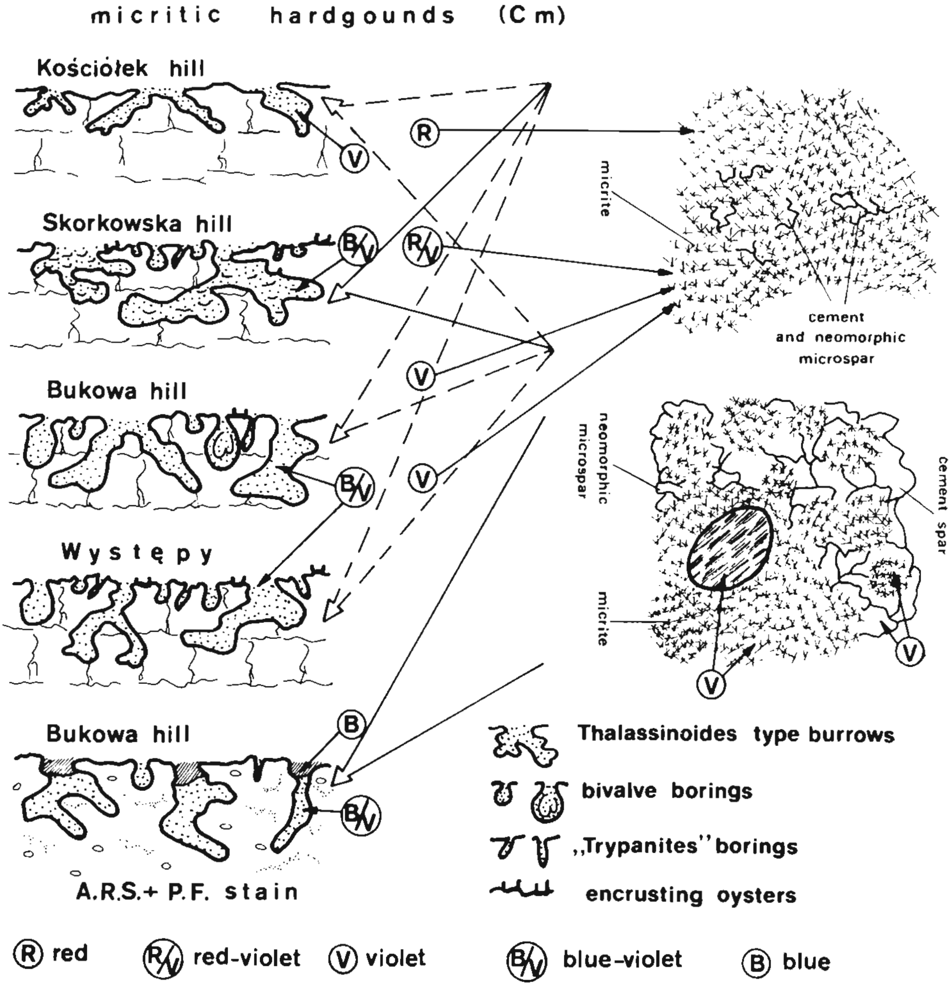

oolitic hardgrounds (Ccg) + (Cg)
Kościołek hill (Ccg)
Piekielnica hill (Cg)
micrite
fibrous fringes
equant-bladed fringe
cement spar
R
V
R/V
B/V
bivalve borings
„Trypanites" borings
encrusted oysters
skeletal detritus
A.R.S. + P.F. stain
R red
V violet
R/V red-violet
B/V blue-violet

oolitic fine-grained hardgrounds (Cfg)




micro-oolitic hardgrounds (C mo)
Występy
B
Kościółek hill
B
Thalassinoides type burrows
bivalve borings
„Trypanites" borings
A. R. S. + P. F. stain
V violet
B/V blue-violet
B blue
bladed
fringes
cement
spar
V
calcite
overgrowths
cement
spar
V
echinoderm fragments
micrite
cement
spar
B/V


micritic - microolite (variant) hardground (Cv)
Thalassinoides type burrows
bivalve borings
encrusting oysters
skeletal detritus
A.R.S. + P.F. stain
R red
R/V red-violet
V violet
V
cement spar
and neomorphic micrite
microspar
R/V
R
cement spar
R/V
V
cement spar
fibrous fringes


micritic hardgounds (Cm)
Kościółek hill
Skorkowska hill
Bukowa hill
Występy
Bukowa hill
A.R.S.+ P.F. stain
R
R/V
V
B/V
B
micrite
cement and neomorphic microspar
neomorphic microspar
cement spar
micrite
Thalassinoides type burrows
bivalve borings
„Trypanites" borings
encrusting oysters
R red
R/V red-violet
V violet
B/V blue-violet
B blue

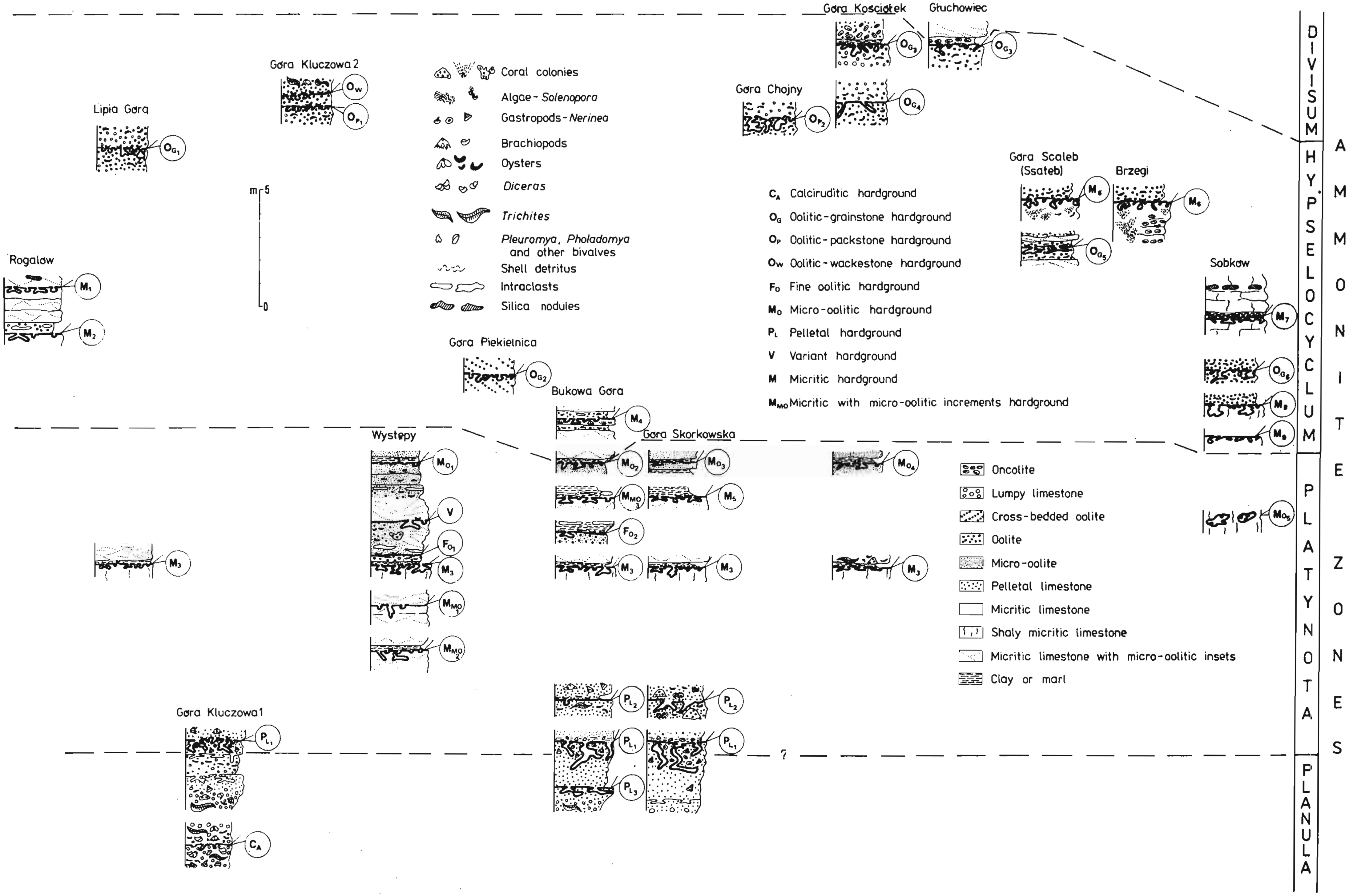


Fig. 3. Distribution of examined hardgrounds within composite sections of upper Jurassic deposits from exposures marked in fig. 1. Stratigraphic divisions are adapted from Kutek (1968).

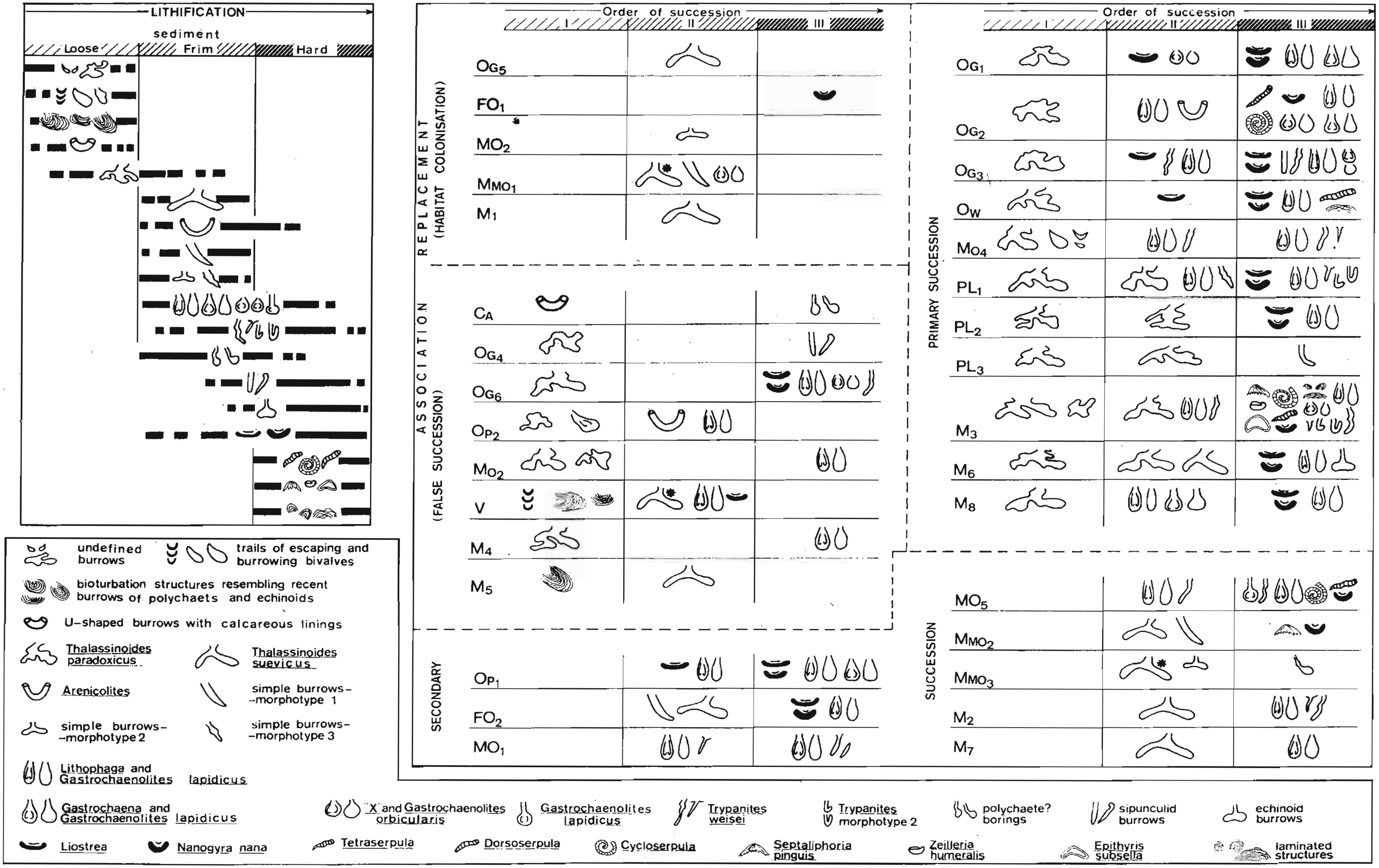


Fig. 4. The first step of ecological succession test of hardgrounds (against first parameter). Possibility of appearance of particular organisms and organic structures in successive links is shown (upper left corner). The relationship between biota and trace fossils associated with examined hardgrounds and stages of bottom sediment consolidation is also shown. The order of succession is attributed to all examined hardground individuals and compared with the model of succession (main diagram). And habitat colonization and false succession, thus association replacement is pointed out. Primary and secondary succession are also marked. Enormous intensity of colonization is marked by stars.

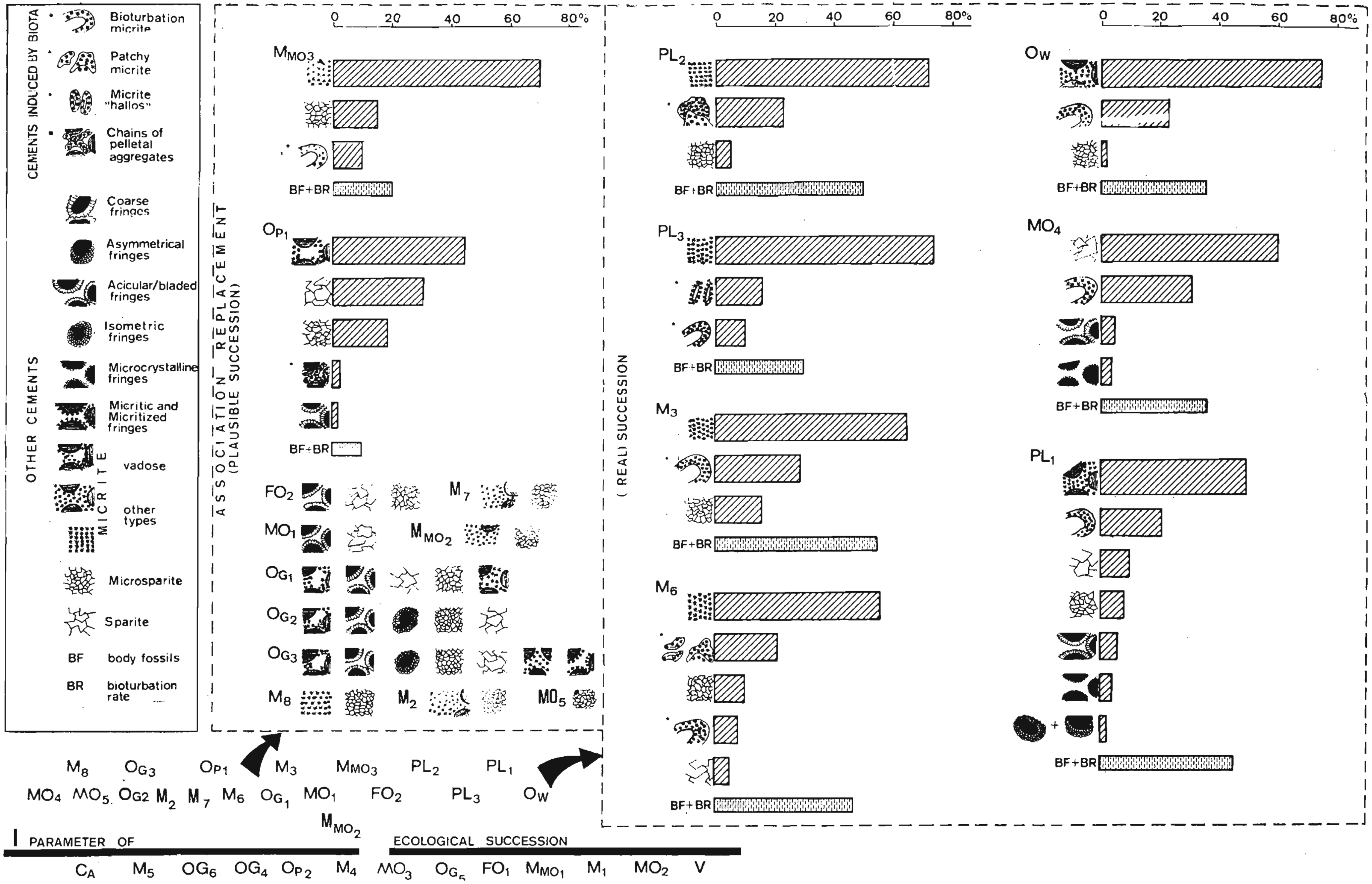


Fig. 5. The second step of ecological succession test of hardgrounds (against second parameter). A lot of types of early diagenetic cements are schematically presented. Cements induced by biota preserved either as the traces or skeletal remains in hardground formations are emphasized (stars). All the cements representative for each single hardground are showed. And the other kind of association replacement, i.e. pseudo- (= plausible) succession and real (= autogenic) succession are distinguished.

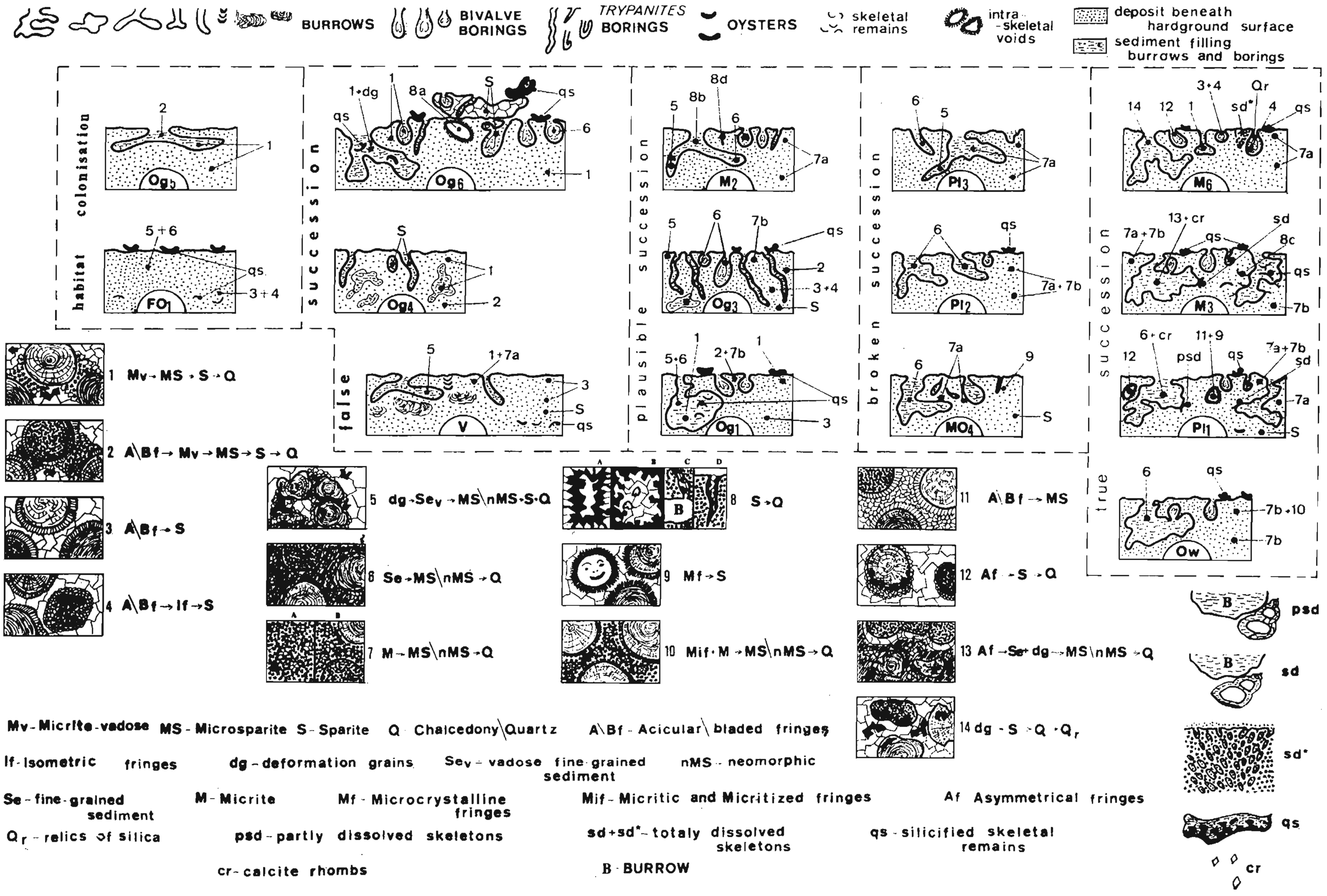


Fig. 10. Cement stratigraphies within the selected hardgrounds are shown. Characteristics of particular grains and skeletal remains is also shown. Note a lot of stages of calcium carbonate solution-precipitation process in conjunction with a lithification of the hardground formations.

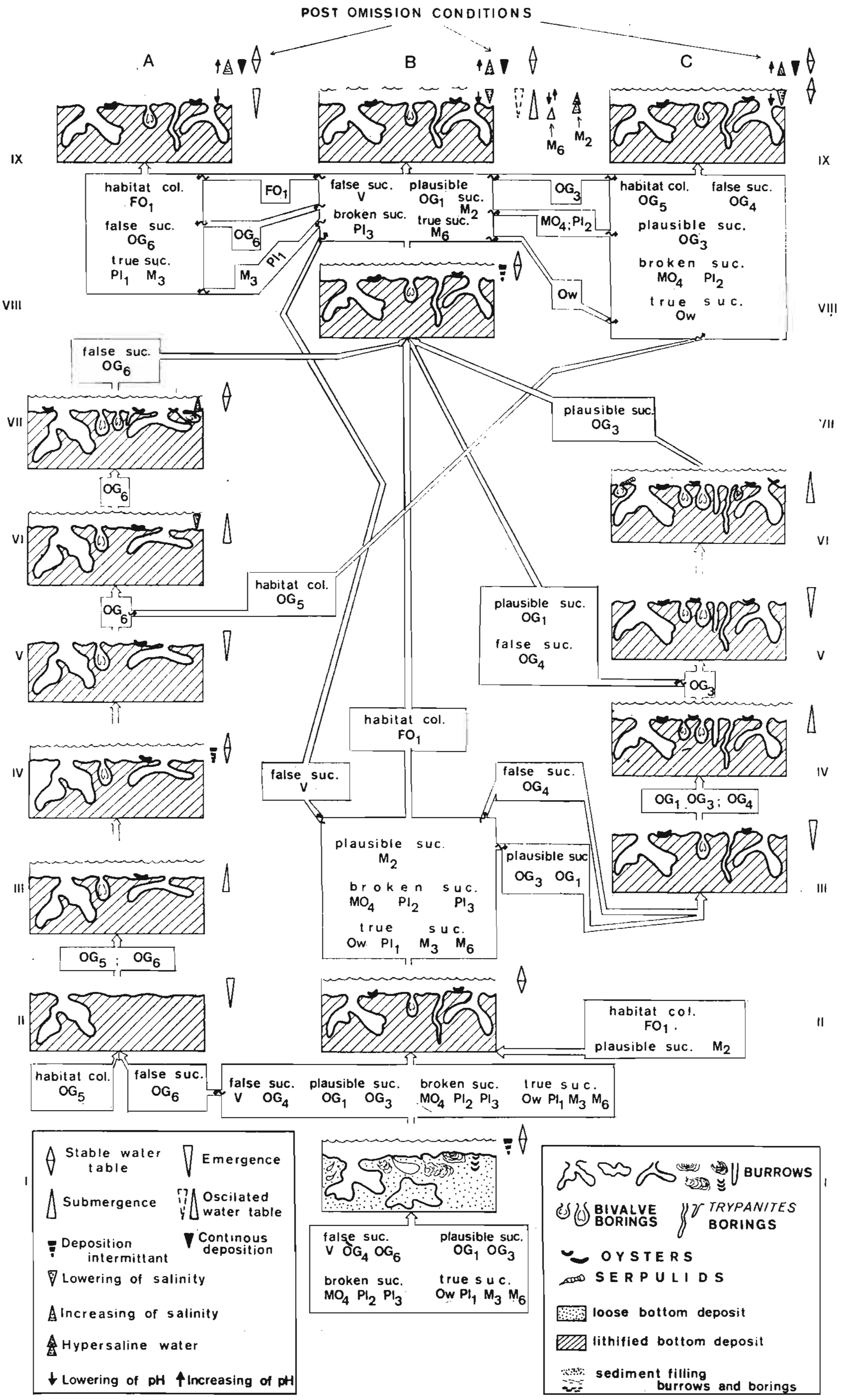


Fig. 12. Identified stages of eogenetic history (from pioneer colonization to final burial) in selected hardgrounds are schematically presented. Note a lot of emersion events in eogenetic history of numerous hardgrounds. Note also changes of pH and salinity at the end of eogenetic history of hardgrounds.

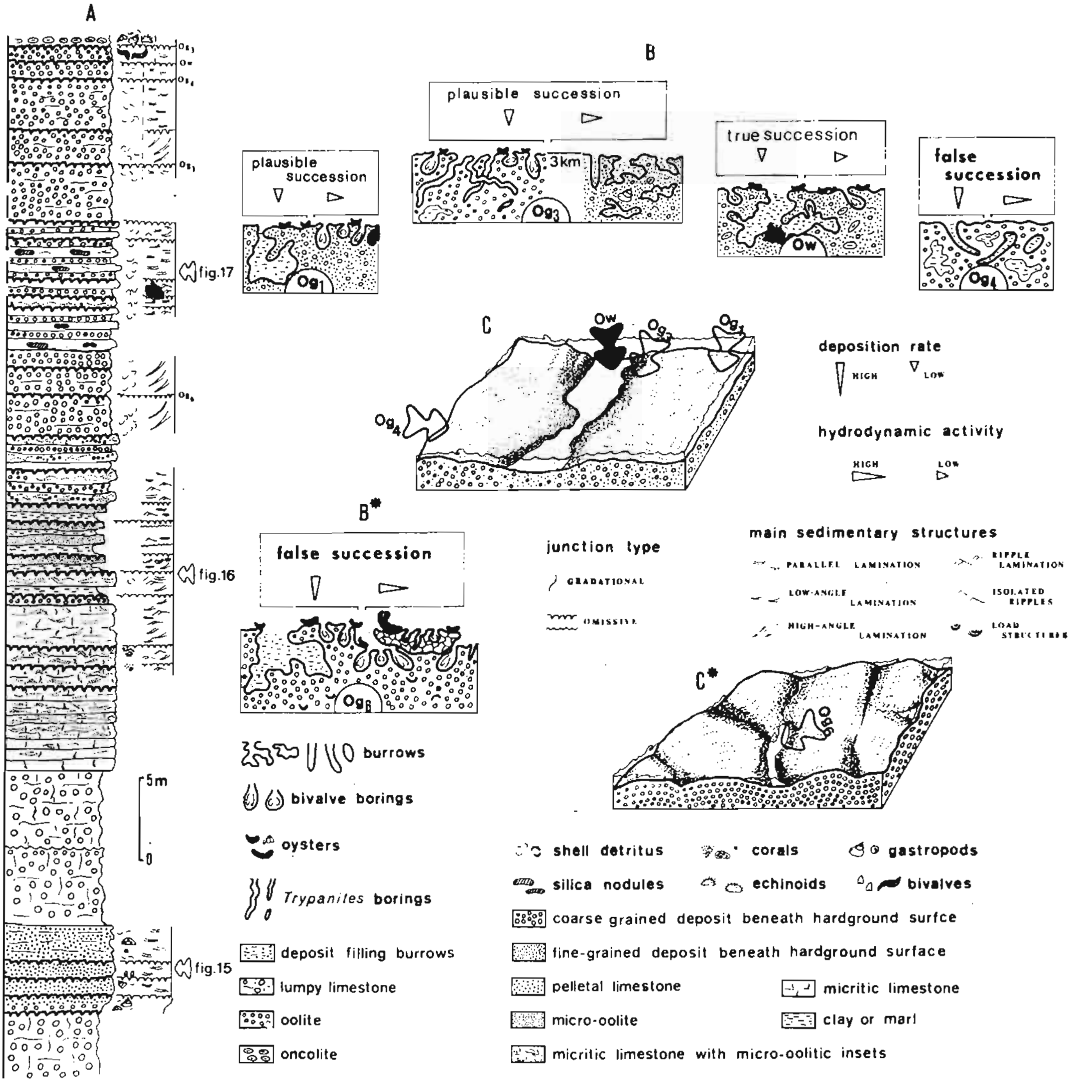
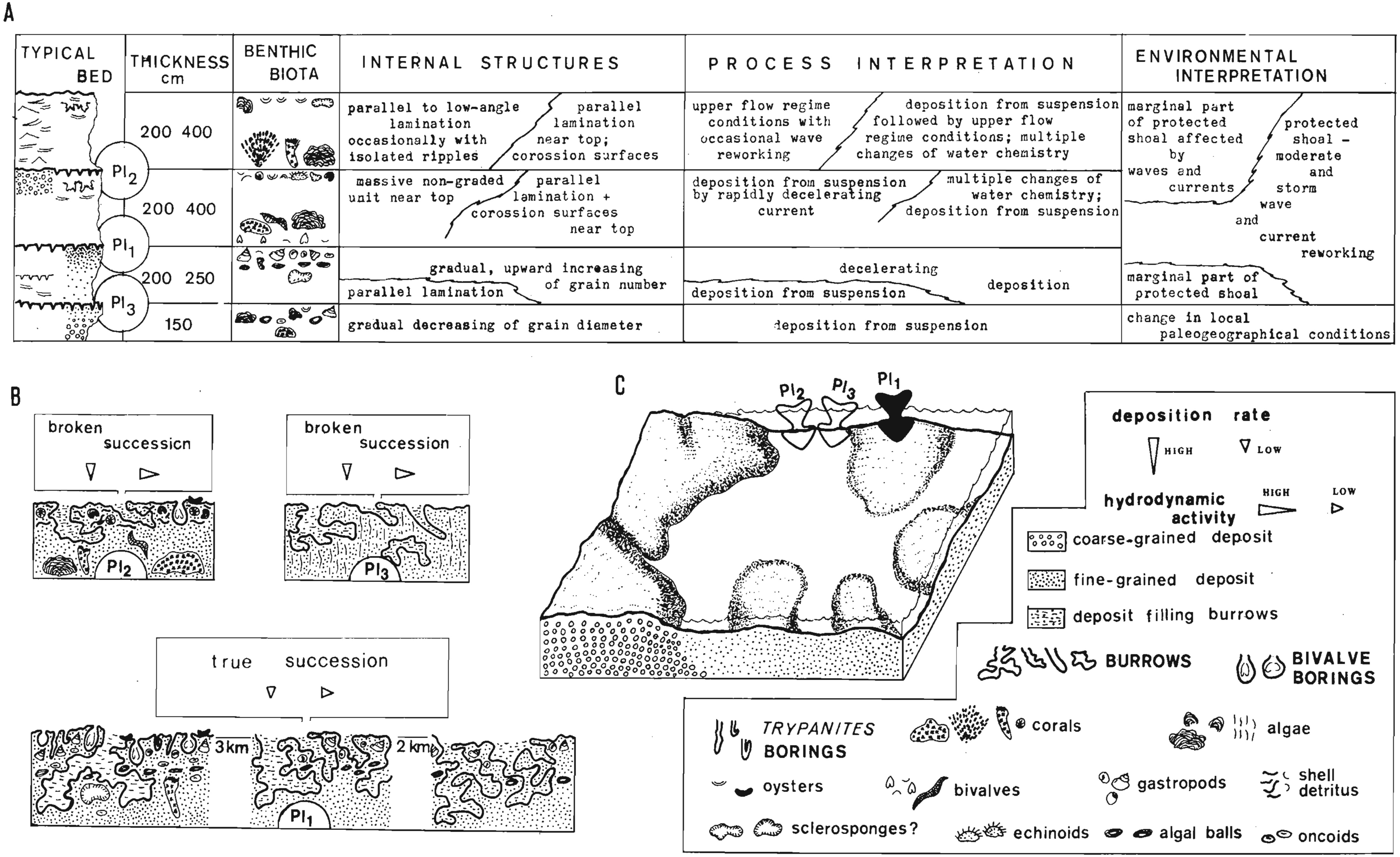


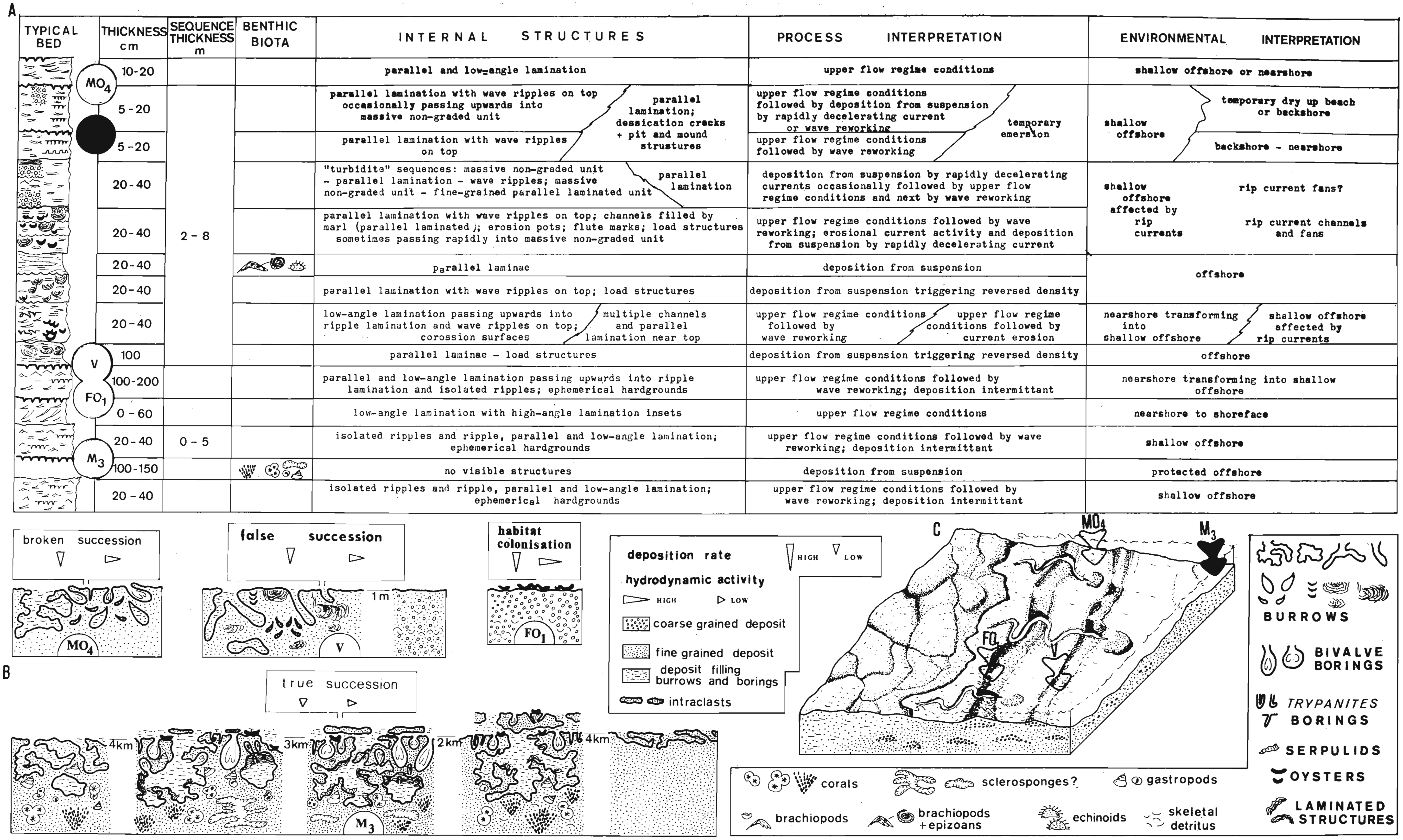
Fig. 14. Environmental context of selected hardground formations. *A* Distribution of sediment sequences examined in details is marked within generalized lithological profile of upper Oxfordian-lower Kimmeridgian deposits representative for studied area. The main internal sedimentary structures are also marked. *B* and *B*+ Sediment and biotic content of hardground formations is schematically presented. Suggested values of hydrodynamic activity and deposition rate are denoted by triangles. C and C+ Sites of development of the hardground formations within imaginable environmental reconstruction are showed. True (= Ecological) succession is denoted by black arrows.



A

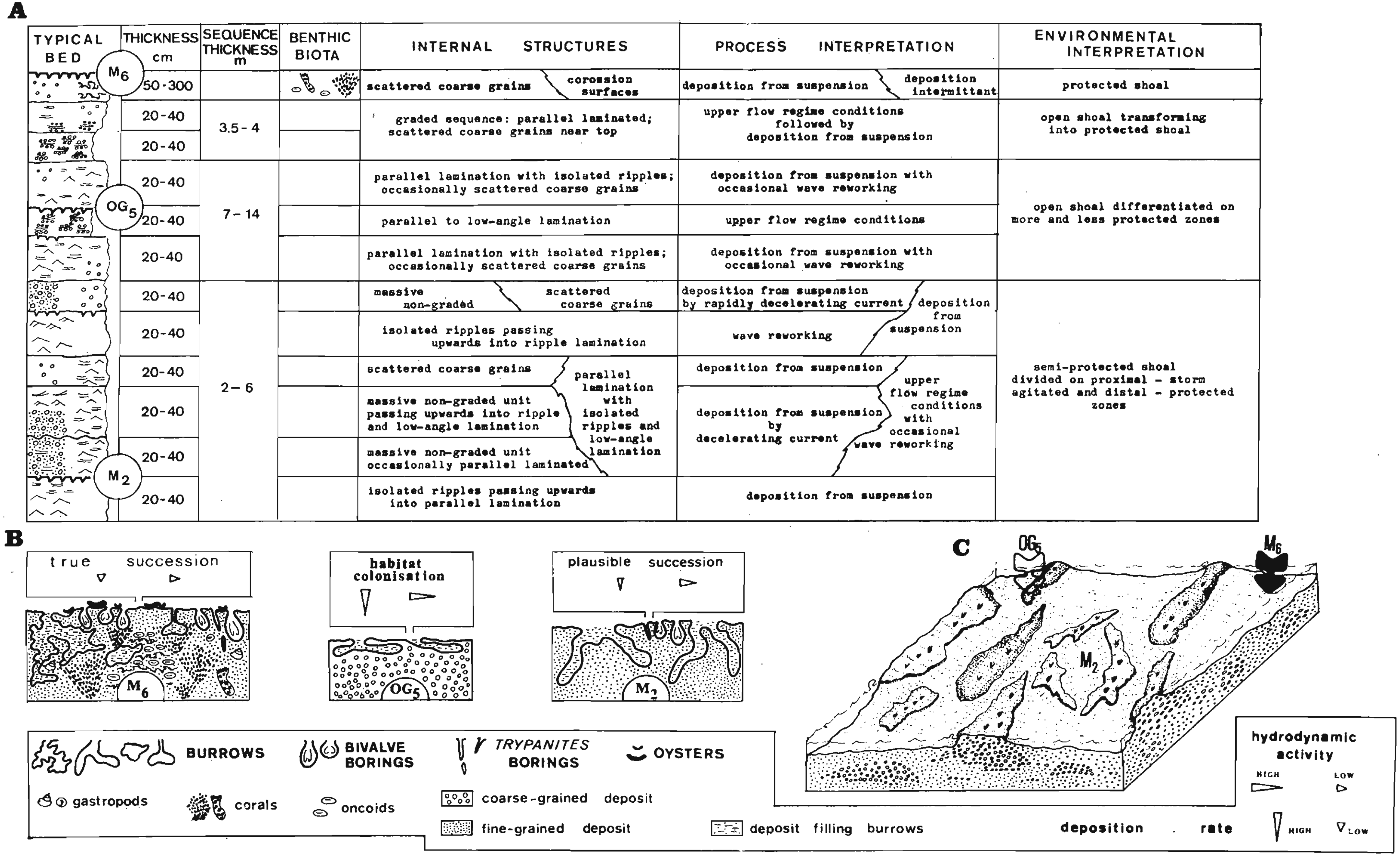
TYPICAL BED	THICKNESS cm	BENTHIC BIOTA	INTERNAL STRUCTURES	PROCESS INTERPRETATION	ENVIRONMENTAL INTERPRETATION
Pl2	200 400		parallel to low-angle lamination occasionally with isolated ripples / parallel lamination near top; corossion surfaces	upper flow regime conditions with occasional wave reworking / deposition from suspension followed by upper flow regime conditions; multiple changes of water chemistry	marginal part of protected shoal affected by waves and currents / protected shoal - moderate and storm wave and current reworking
Pl1	200 400		massive non-graded unit near top / parallel lamination + corossion surfaces near top	deposition from suspension by rapidly decelerating current / multiple changes of water chemistry; deposition from suspension	
Pl3	200 250		parallel lamination / gradual, upward increasing of grain number	deposition from suspension / decelerating deposition	marginal part of protected shoal
	150		gradual decreasing of grain diameter	deposition from suspension	change in local paleogeographical conditions

Fig. 15. Environmental context of selected hardground formations. *A* Environmental interpretation is presented on the basis of internal sedimentary structures analysis and observations of the skeletal remains within examined sediments. *B* Sediment and biotic content of hardground formations is schematically presented. Suggested values of hydrodynamic activity and deposition rate are denoted by triangles. *C* Sites of development of hardground formations within imaginable environmental reconstruction are showed. True (= Ecological) succession is denoted by black arrow.



TYPICAL BED	THICKNESS cm	SEQUENCE THICKNESS m	BENTHIC BIOTA	INTERNAL STRUCTURES	PROCESS INTERPRETATION	ENVIRONMENTAL INTERPRETATION
MO4	10-20			parallel and low-angle lamination	upper flow regime conditions	shallow offshore or nearshore
	5-20	2 - 8		parallel lamination with wave ripples on top occasionally passing upwards into massive non-graded unit parallel lamination; dessication cracks + pit and mound strustures	upper flow regime conditions followed by deposition from suspension by rapidly decelerating current or wave reworking temporary emersion	shallow offshore temporary dry up beach or backshore
●	5-20			parallel lamination with wave ripples on top	upper flow regime conditions followed by wave reworking	backshore - nearshore
	20-40			"turbidite" sequences: massive non-graded unit - parallel lamination - wave ripples; massive non-graded unit - fine-grained parallel laminated unit parallel lamination	deposition from suspension by rapidly decelerating currents occasionally followed by upper flow regime conditions and next by wave reworking	shallow offshore affected by rip currents rip current fans?
	20-40			parallel lamination with wave ripples on top; channels filled by marl (parallel laminated); erosion pots; flute marks; load structures sometimes passing rapidly into massive non-graded unit	upper flow regime conditions followed by wave reworking; erosional current activity and deposition from suspension by rapidly decelerating current	rip current channels and fans
	20-40			parallel laminae	deposition from suspension	offshore
	20-40			parallel lamination with wave ripples on top; load structures	deposition from suspension triggering reversed density	
	20-40			low-angle lamination passing upwards into ripple lamination and wave ripples on top; corossion surfaces multiple channels and parallel lamination near top	upper flow regime conditions followed by wave reworking upper flow regime conditions followed by current erosion	nearshore transforming into shallow offshore shallow offshore affected by rip currents
V	100			parallel laminae - load structures	deposition from suspension triggering reversed density	offshore
FO1	100-200			parallel and low-angle lamination passing upwards into ripple lamination and isolated ripples; ephemerical hardgrounds	upper flow regime conditions followed by wave reworking; deposition intermittant	nearshore transforming into shallow offshore
	0 - 60			low-angle lamination with high-angle lamination insets	upper flow regime conditions	nearshore to shoreface
	20-40	0 - 5		isolated ripples and ripple, parallel and low-angle lamination; ephemerical hardgrounds	upper flow regime conditions followed by wave reworking; deposition intermittant	shallow offshore
M3	100-150			no visible structures	deposition from suspension	protected offshore
	20 - 40			isolated ripples and ripple, parallel and low-angle lamination; ephemerical hardgrounds	upper flow regime conditions followed by wave reworking; deposition intermittant	shallow offshore

Fig. 16. Environmental context of selected hardground formations. *A* Environmental interpretation is presented on the basis of internal sedimentary structures analysis and observations of the skeletal remains within examined sediments. *B* Sediment and biotic content of hardground formations is schematically presented. Suggested values of hydrodynamic activity and deposition rate are denoted by triangles. *C* Sites of development of hardground formations within imaginable environmental reconstruction are showed. True (= Ecological) succession is denoted by black arrow.



A

TYPICAL BED	THICKNESS cm	SEQUENCE THICKNESS m	BENTHIC BIOTA	INTERNAL STRUCTURES	PROCESS INTERPRETATION	ENVIRONMENTAL INTERPRETATION
M_6	50-300			scattered coarse grains corossion surfaces	deposition from suspension deposition intermittant	protected shoal
	20-40	3.5-4		graded sequence: parallel laminated; scattered coarse grains near top	upper flow regime conditions followed by deposition from suspension	open shoal transforming into protected shoal
	20-40					
	20-40	7-14		parallel lamination with isolated ripples; occasionally scattered coarse grains	deposition from suspension with occasional wave reworking	open shoal differentiated on more and less protected zones
OG_5	20-40			parallel to low-angle lamination	upper flow regime conditions	
	20-40			parallel lamination with isolated ripples; occasionally scattered coarse grains	deposition from suspension with occasional wave reworking	
	20-40	2-6		massive non-graded scattered coarse grains	deposition from suspension by rapidly decelerating current deposition from suspension	semi-protected shoal divided on proximal - storm agitated and distal - protected zones
	20-40			isolated ripples passing upwards into ripple lamination	wave reworking	
	20-40			scattered coarse grains parallel lamination with isolated ripples and low-angle lamination	deposition from suspension upper flow regime conditions with occasional wave reworking	
	20-40			massive non-graded unit passing upwards into ripple and low-angle lamination	deposition from suspension by decelerating current	
	20-40			massive non-graded unit occasionally parallel laminated		
M_2	20-40			isolated ripples passing upwards into parallel lamination	deposition from suspension	

Fig. 17. Environmental context of selected hardground formations *A* Environmental interpretation is presented on the basis of internal sedimentary structures analysis and observations of the skeletal remains within examined sediments. *B* Sediment and biotic content of hardground formations is schematically presented. Suggested values of hydrodynamic activity and deposition rate are denoted by triangles. *C* Sites of development of hardground formations within imaginable environmental reconstruction are showed. True (= Ecological) succession is denoted by black arrow.