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## Sedimentary environment and synecology of macrobenthic assemblages of the marly sands and red-algal limestones in the Korytnica Basin (Middle Miocene; Holy Cross Mountains, Central Poland)

**ABSTRACT:** The facies development of the upper part of the Middle Miocene (Badenian) sedimentary sequence of the Korytnica Basin (Holy Cross Mountains, Central Poland) was controlled by high hydrodynamic activity (storms) and diversified bathymetric conditions. Deposition of red-algal limestones on the rocky submarine ridges and marly sands in the deeper parts of the Basin took place in that shallow, nearshore marine environment. Synecological analysis of the macrobenthic *Acanthocardia* assemblage of the marly sands shows very high dominance of the lower level infaunal suspension feeders, among which one bivalve species, *Acanthocardia paucicostata* (Sowerby), represents nearly 34% of the total biovolume. Infauna was dominated by very rapid burrowers adapted to unstabilized environment. The red-algal bank community was composed primarily of epifaunal browsers and suspension feeders.

### INTRODUCTION

The Korytnica Basin is a small part of the Korytnica Bay developed during the Middle Miocene (Badenian) transgression onto the southern slopes of the Holy Cross Mountains (see RADWAŃSKI 1969; BAŁUK & RADWAŃSKI 1977, 1979).

The Badenian sedimentary sequence of the Korytnica Basin can be briefly summarized (cf. RADWAŃSKI 1969, BAŁUK & RADWAŃSKI 1977, SZYMANKO & WÓJCIK 1982) as follows: it begins with accumulation of brown-coal deposits covered by green clays turning upwards into the Korytnica Clays which contain the world-famous, mollusk-dominated fauna. The marly sands and red-algal limestones discussed in this paper overlie directly the Korytnica Clays. Analysis of the calcareous nannoplankton (MARTINI 1977) shows that the Korytnica Clays and overlying marly sands are of Middle Badenian age (zones NN 5 and NN 6).

Synecological analysis of the macrobenthic fossil assemblages is now popular among paleontologists. However, the methods adopted for paleoecological studies by WALKER (1972) allow only to a more or less simplified reconstruction of ancient communities, being first of all proper for interpretation of sedimentary environments. This work is thought to be a following test of ecological theory, in the fossil record, and it continues former synecological investigations of the Korytnica Basin (HOFFMAN 1977, 1979).

#### MEMBERS OVERLYING THE KORYTNIKA CLAYS

Near the village Korytnica (locality 1 in Text-fig. 1), the topmost part of the Korytnica Clays which contain many intercalations of coherent marls or marly sandstones (unit 1 in Text-fig. 2A), pass gradually into grey marly sands (unit 2 in Text-fig. 2A; cf. KOWALEWSKI 1930, RADWAŃSKI 1969). In the upper part of unit 2 (see Text-fig. 2A) all the fossils bearing primary aragonite shells appear only as the imprint

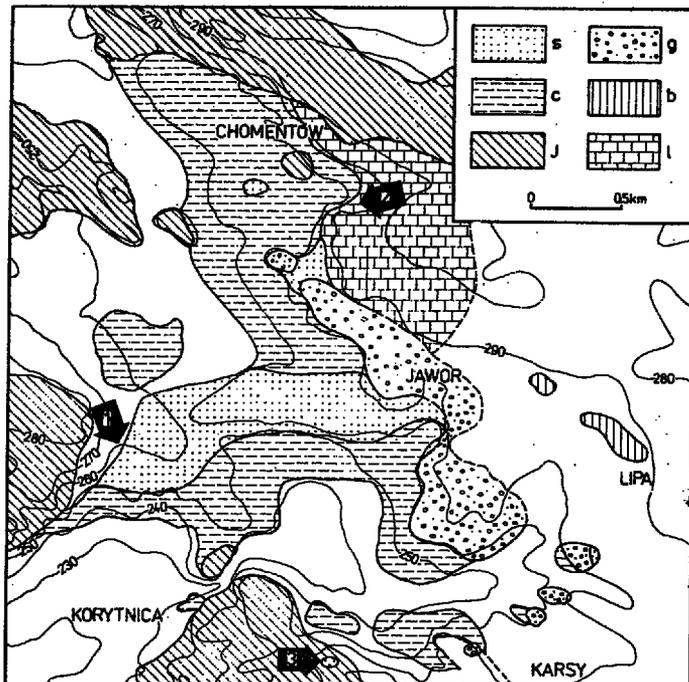


Fig. 1. Geological sketch-map of the Korytnica Basin (compiled from: KOWALEWSKI 1930, DAWIDOWSKI 1974, and personal observations)

J — Jurassic substrate, c — Korytnica Clays, s — marly sands, l — red-algal limestones, b — sandy red-algal deposits with bentonites, g — gravels ("detrital Sarmatian", cf. GUTOWSKI 1983); Quaternary deposits are blank

Localities described in the text: 1 — Korytnica, 2 — Chomentów, 3 — newly discovered locality of littoral structures (GUTOWSKI & MACHALSKI 1984)

and/or moulds. This makes an important difference between the Korytnica Clays (cf. BAŁUK & RADWAŃSKI 1977) and all the overlying deposits. Large foraminifers *Heterostegina* and *Amphistegina*, oval red-algal nodules (rhodoids, as named by PERYT, 1983) and debris of echinoids, asteroids, bivalves and other calcite-skeletal organisms are very common within units 2—5, especially within the *Heterostegina* sands (unit 5 in Text-fig. 2A).

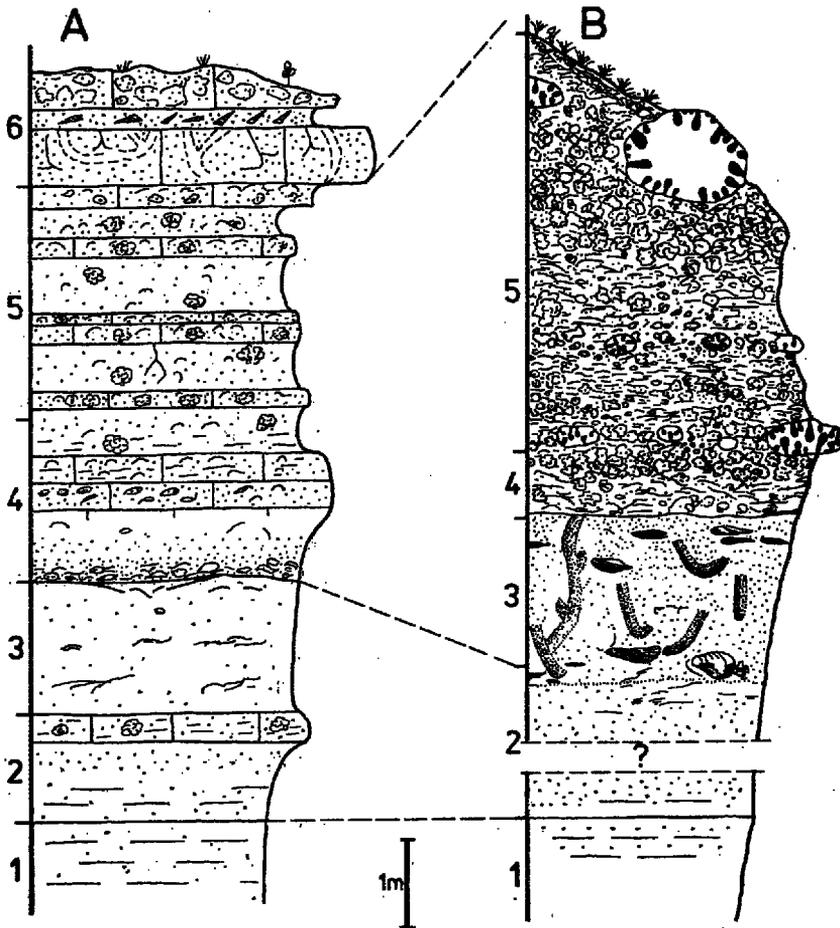


Fig. 2. Deposits overlying the Korytnica Clays in the Korytnica Basin.

A — Deposits exposed at Korytnica: 1 — Korytnica Clays, 2 — grey marly sands, 3 — yellow sands with red-algal detritus, 4 — sandy marls with accumulation of Jurassic pebbles and red-algal detritus at the base, 5 — *Heterostegina* sands with intercalations of sandstones yielding abundant fossils, 6 — sandstones with burrows, and with red-algal glauconitic limestones at the top

B — Deposits exposed at Chomentów (after RADWAŃSKI 1977; completed): 1 — Korytnica Clays, 2 — marly sands poor in fauna, 3 — marly sands with crab burrows and abundant fossils, 4 — red-algal limestones with marly sand (in lower part: a thin lamina of floral detritus), 5 — red-algal limestones with boulders bored by rock-borers

Unit 3 (Text-fig. 2A) is composed of yellow, well cemented sands. The red-algal material occurs here only in form of fine detritus, which sometimes marks the bedding surfaces. Fine gravel material (up to 5 mm in diameter) of Jurassic pelitic limestones and cherts appears also occasionally. A thin layer, which consists of red-algal detritus, sand and abundant gravel material (up to 5 cm in diameter) derived from local Jurassic basement, rests at the rough upper surface of unit 3. The pebbles are sometimes bored by diverse rock-borers. This unit is overlain by white-grey sandy marls (unit 4 in Text-fig. 2A).

In the middle part of unit 4, fine-grained sandstone crowded with fine red-algal detritus and tubes of ditrupid polychaetes is present. Shells of some bivalves, including large *Panopea menardi* (DESHAYES)<sup>1</sup>, are accumulated on some layer surfaces. In other parts of the sequence, this *Panopea* species occurs only in its life position.

The thickest unit 5 (Text-fig. 2A) is composed of ash-yellow, fine-grained marly sands which contain very abundant fossils. The marly sandstones with platy accumulations of fauna, primarily bivalves dominated by *Acanthocardia paucicostata* (SOWERBY) make often intercalations within the limits of these sands (KOWALEWSKI 1930, RADWAŃSKI 1969).

The topmost part of the sequence is taken by limy sandstones with various biogenic burrows, and by red-algal limestones which contain autigenic glauconite and mass-aggregated moulds of shells of the gastropod *Turritella* sp.

The section exposed at Chomentów (locality 2 in Text-fig. 1) was analysed in detail by RADWAŃSKI (1969, 1977; see Text-fig. 2B).

#### FACIES DEVELOPMENT

The first depositional stage of the members overlying the Korytnica Clays (A in Text-fig. 3) was characterized by relatively quiet sedimentation in a low-energy environment. This stage is represented by units 1—3 at Korytnica (Text-fig. 2A) and units 1—2 at Chomentów (Text-fig. 2B). A gradually increasing delivery of sandy material was probably a result of slow intensification of the tectonic upheaval of the Holy Cross shores.

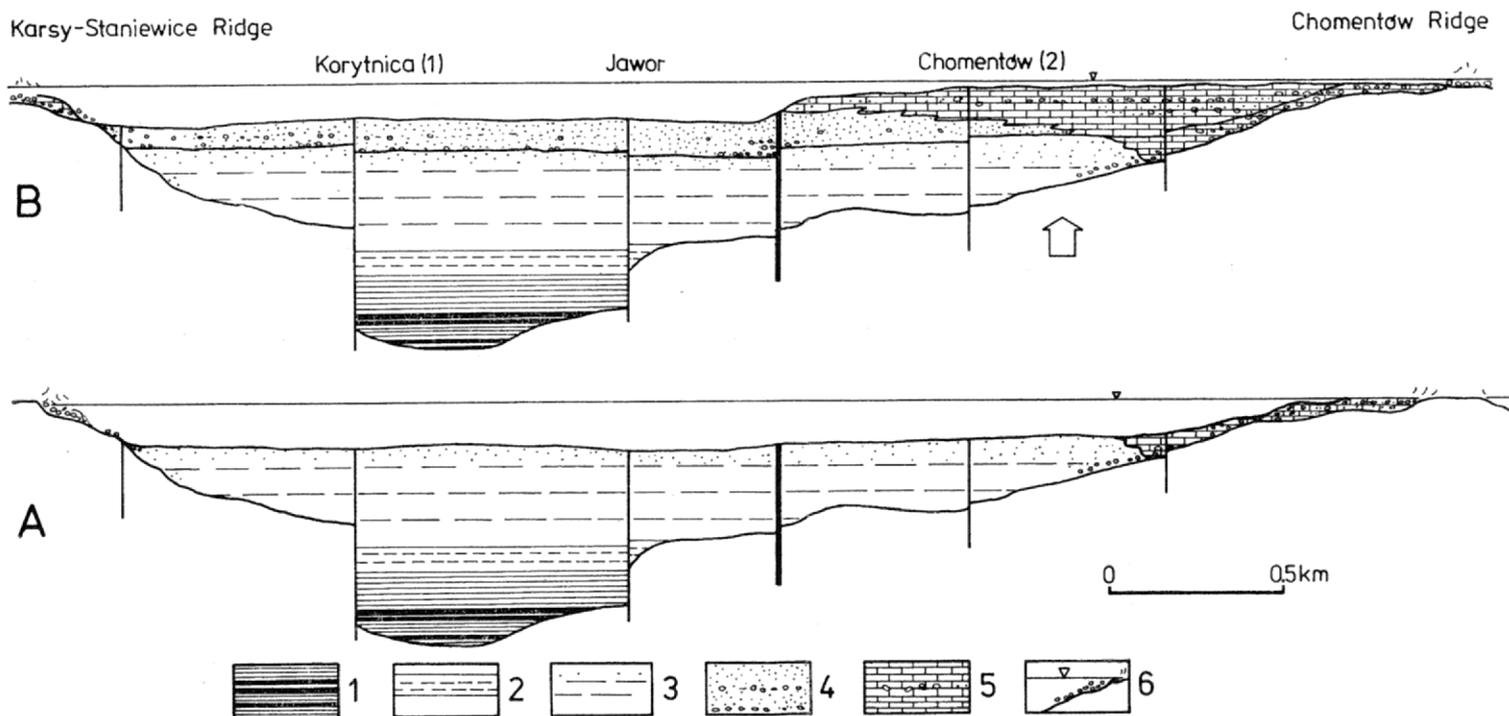
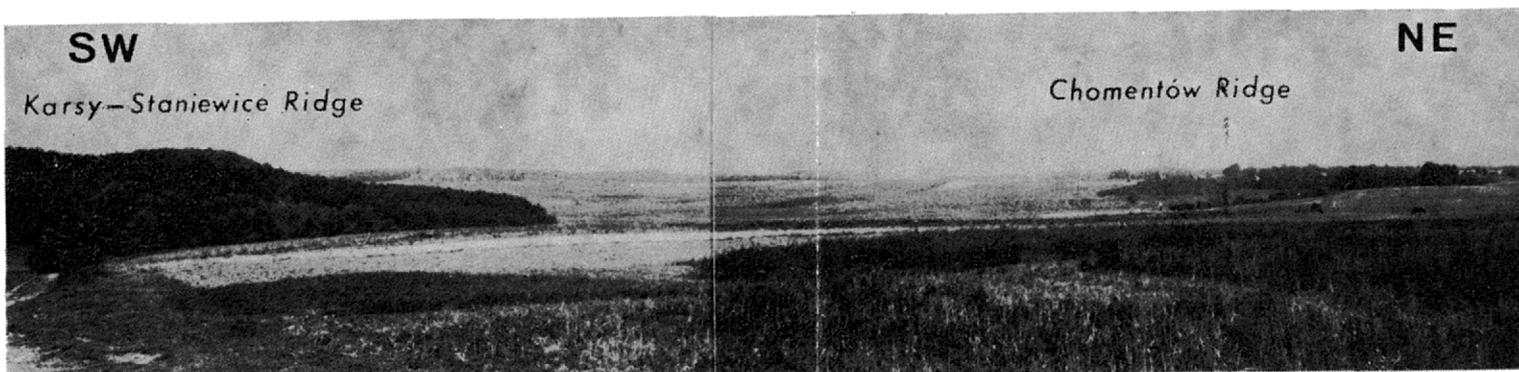
The terrigenous material was accumulated in the deeper, central part of the Basin, whereas along marginal rocky ridges (see stage A in Text-fig. 3) the red-algal limy deposit was laid down. These shores, i. e. the

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<sup>1</sup> All the bivalves are classified according to recent taxonomic investigations of STUDENCKA (1985).

### Idealized cross-sections trough the Korytnica Basin

**A** — At time of deposition of the marly sands, **B** — At time of deposition of the red-algal limestones; thickness proportion given approximately, vertical scale five times exaggerated; overlying is the present-day landscape of the Korytnica Basin



1 — brown coal deposits, 2 — green clays, 3 — Korytnica Clays (in their upper part: intercalations of marls and sandstones), 4 — marly sands with faunal accumulations, pebbles and single rhodoids, 5 — red-algal limestones containing large boulders derived from the shore, 6 — abrasion zones along the shore built of Jurassic limestones

Chomentów Ridge on NE and Karsy-Staniewice Ridge on SW, yielded convenient places for development of the red-algal communities (cf. GUTOWSKI & MACHALSKI 1984).

In the following stage (B in Text-fig. 3), a rapid increase of hydrodynamic activity took place in the Basin. Such a phenomenon, caused by diastrophic and/or climatic reasons, was previously observed in profiles of the same stratigraphic position ("Lower Opolian") in the eastern and south-eastern margins of the Holy Cross Mountains, i. e. in the Opatów Bay and along the Raków-Klimontów Shore (RADWAŃSKI 1970, 1973).

The marly sands (units 4—5 in Text-fig. 2A) are considered as typical of the shallow marine environment, occasionally subjected to the storms (cf. RHOADS 1975, p. 157, Text-fig. 9.8, example 7). The faunal accumulations (Pl. 1, Figs 1—2) can be interpreted as deposited during storm events. Winnowing of bottom sediments, washing out of infaunal organisms and development of coquinal lags took place at that time. Some of the storm events must have been strong enough to wash out the shells of *Panopea menardi* (DÉSHAYES) which lived about 1 m below the sediment/water interface.

Characteristic oval shape of the rhodoids (Pl. 2, Figs 3—4) developed around the shells or pebbles seems to have been caused by their rolling under high hydrodynamic conditions (cf. BOSENCE 1983).

The majority of bivalve valves has been arranged convex-side up on the surface of sandstone layers, but any linear current structures have not been observed. Thus, a high turbulence of storm nature (cf. FUTTERER 1974) may be inferred.

Because any tidal sedimentary structures are lacking within the marly sands at Chomentów (units 3—4 in Text-fig. 2B; cf. RADWAŃSKI 1977), the environment occupied by burrowing crabs cannot be simply compared to the recent tidal coast of Georgia and Bahama (cf. SHINN 1968, FREY & MAYOU 1971). The Miocene crabs lived in the Korytnica Basin on a flat, sandy offshore banks occasionally visited by storms (cf. RADWAŃSKI 1977). A thin lamina of floral detritus which was probably derived from the coast during a heavy storm, is also seen in the topmost part of the sands.

The Korytnica Basin was subdivided into two parts during sedimentation of the discussed deposits (see stage B in Text-fig. 3): the shallow one with red-algal deposits (Chomentów zone) and relatively deeper one (Korytnica zone) with the *Heterostegina* sand facies (see Text-fig. 2; and RADWAŃSKI 1969, BAŁUK & RADWAŃSKI 1977). The boundary between these two zones was of synsedimentary tectonic nature (SZYMANKO & WÓJCIK 1982). The tendency to the lowering of the central part of the Basin (Korytnica zone) has led to inhibition of carbonate platform development.

An increasing delivery of red-algal detritus from the Chomentów Ridge to the deeper part of the Basin (unit 4 in Text-fig. 2B) should be treated as a consequence of high hydrodynamic activity at that time. Stratigraphically above, detrital red-algal limestones composed mostly of rhodoids and of fragments of open-branched coralline thalli was deposited. The bottom was accessible for a prolific autochthonous growth of the corallines, which supposedly formed a bank (cf. BOSENCE 1976). During the storm events the coralline structures were destroyed and reworked. Simultaneously, littoral pebbles and boulders up to 1.1 m in diameter were delivered from the Chomentów Ridge (see RADWAŃSKI 1969, 1970, 1977).

In somewhat greater (about 10 m) depths of the Korytnica zone, the sandy terrigenous material was accumulated. It contains only insignificant content of red-algal detritus. The unstabilized sandy bottom could not have been accessible for development of red-algal banks. The red algae have only overgrown the shells or smaller rock pieces and have produced single discoidal and/or spheroidal rhodoids (Pl. 1, Fig. 2).

#### ECOLOGICAL ANALYSIS OF THE ACANTHOCARDIA ASSEMBLAGE

The samples, together about 80 kg of the deposit, were taken from one of the layers of the *Heterostegina* sands (unit 5 in Text-fig. 2A), which can be approximately studied as an isochronous surface. They have been washed by a mesh screen of 2 mm and all the skeletal remains have been collected. The moulds and imprints of original aragonite shells have been numbered from the equal sample of the sandstone interbedded within the sands. Higher moulds density within the sandstone has been taken into account in the calculation. In addition, one sample about 3 kg of the deposit has been washed by a mesh screen of 0.3 mm to recognize the microfossils.

A comparative element of the biovolume was the volume of moderate large moulds. Such a procedure seems to be more adequate than to compare the volume (weight) of preserved skeletal remains (e. g. shells) because it takes into account various proportions of the soft body to the skeletal preservable parts of several organisms (e. g. asteroids and oysters).

#### TAXONOMIC COMPOSITION, DIVERSITY AND DENSITY

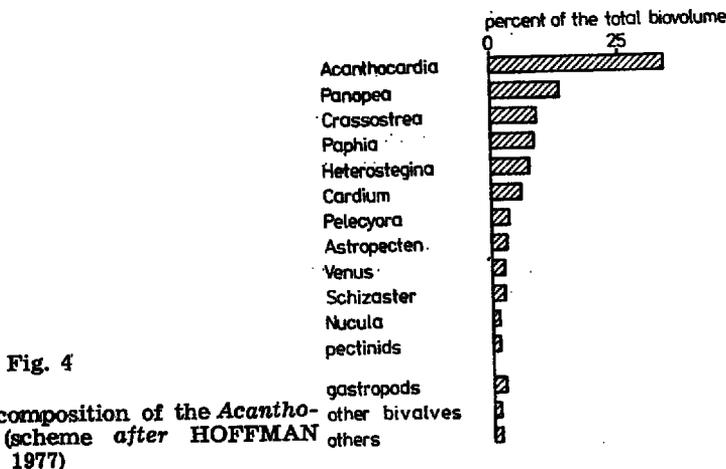
Diversity of the *Acanthocardia* assemblage is high; it includes about 70 macrobenthic species, i. a. 28 species of bivalves and 15 species of gastropods (see Table 1). The density may also be estimated as high.

Within the foraminifers, large foraminifer *Heterostegina* dominates and, taking into account its size (up to 1 cm) and abundance, it is included into the trophic analysis. Additionally, amphisteginids, elphidiids, anomalinids and cibicids occur frequently, and are associated with miliolids, nodosariids and globigerinids, as well as with many ostracodes and holothurian sclerites. Benthic flora is represented by single rhodoids (Pl. 1; Fig. 2). Fishes played in the ecosystem probably an important role, because their teeth and other skeletal remains (see Table 2) appear within the assemblage. The lack of fish otoliths can be explained by selective dissolution of aragonite. Badly preserved fragments of diverse burrows attributable to crabs, echinoids and polychaetes are recognizable in some places.

In these horizons of the deposits overlying the Korytnica Clays (see unit 5 in Text-fig. 2A), the abundance and diversity of the assemblage reaches their maximum. Both the bivalve shells often preserved with their valves opened (Pl. 2, Fig. 2) and numerous individuals found in life position (*Panopea*, *Paphia*, *Solen*) suggest a lack of any significant *post-mortem* sorting or transportation, and preservation of fossils in about the same proportion as when they were alive (cf. JOHNSON 1960, FAGERSTROM 1964, STANTON 1976).

#### DISPERSION OF THE BIOVOLUME

Although the taxonomic diversity is high, one species of the bivalves, *Acanthocardia paucicostata* (SOWERBY), represents nearly 34% of the total biovolume (see Text-fig. 4). Together with four other bivalve species, such as *Panopea menardi*



(DESHAYES), *Crassostrea gryphoides* (SCHLOTHEIM), *Paphia vetula* (BASTEROT), and *Cardium hians danubianum* MAYER, and foraminifers of the genus *Heterostegina*, it constitutes nearly 80% of the total biovolume. The trophic nucleus is also distinctly homogenous and consists mainly of infaunal suspension feeders\* (Text-figs 5—6).

The *Acanthocardia* assemblage makes up an opposite example when compared to the *Turboella-Loripes* assemblage from the upper part of the Korytnica Clays,

\* The feeding types of benthic taxa are categorized accordingly to classification given by WALKER & BAMBACH (1974).

Table 1

Mollusks occurring in the deposits overlying the Korytnica Clay  
Exclamation marks indicate very abundant species

	Korytnica	Chomentów	
		marly sands	red-algal limestones
<b>BIVALVIA</b>			
<i>Nucula</i> sp.	+!		
<i>Barbatia</i> cf. <i>lingua</i> Fuchs	+		
<i>Atrina radwanskii</i> Jakubowski	+	+	
<i>Chlamys scabrella</i> (Lamarck)	+	+	+!
<i>Chlamys latissima nodosiformis</i> (Serres in Pusch)	+	+	+
<i>Flabellipecten solarium</i> (Lamarck)	+		
<i>Pododesmus squamulus</i> (Linnaeus)	+	+	
<i>Crassostrea gryphoides</i> (Schlotheim)	+!	+!	
<i>Cubitostrea digitalina</i> (Eichwald, emend. du Bois)	+	+	
<i>Loripes</i> sp.	+		
<i>Lucinoma borealis</i> (Linnaeus)	+		
<i>Lima</i> sp.	+		
<i>Acanthocardia paucicostata</i> (Sowerby)	+!	+	
<i>Cardium hians danubianum</i> Mayer	+	+	
<i>Pholadomya alpina</i> Matheron	+		
? <i>Lutraria</i> sp.	+		
<i>Tellina</i> sp.	+		
<i>Solecurtus basteroti</i> des Moulins	+		
<i>Solen</i> sp.	+		
<i>Teredo</i> cf. <i>norvegica</i> Spengler	+		
<i>Venus multilamella</i> Lamarck	+	+	
<i>Circomphalus subplicatus</i> (d'Orbigny)	+		
<i>Pelecyora islandicoides</i> (Lamarck)	+	+	
<i>Pelecyora gigas</i> (Lamarck)	+	+	
<i>Paphia vetula</i> (Basterot)	+!	+!	
<i>Corbula gibba</i> (Olivi)	+	+	
<i>Panopea menardi</i> (Deshayes)	+!	+!	
<i>Gastrochaena</i> sp.		+	+
<i>Aspidopholas</i> sp.			+
<i>Lithophaga</i> sp.			+
<b>GASTROPODA</b>			
Trochidae			+
<i>Petalococonchus intortus</i> (Lamarck)	+	+	+
<i>Turritella</i> sp.	+		
<i>Scala kostejana</i> (Boettger)	+	+	+
<i>S. spinosa</i> Bonelli	+	+	
<i>Acrilla orientalis</i> (Friedberg)	+	+	
<i>Calyptrea</i> sp.	+		
<i>Natica</i> sp.	+		
<i>Aporrhais pespelecani</i> (Lamarck)	+		
<i>Cassis</i> sp.	+		
? <i>Lyrta</i> sp.	+		
<i>Pyrula condita</i> Brongniart	+		
<i>Triton nodiferum</i> Lamarck	+		
<i>Triton affine</i> Deshayes	+		
<i>Nassa</i> sp. div.	+		

Table 2

Non-mollusk taxa from the deposits overlying the Korytnica Clays  
 Brachiopods are determined after BARCZYK & POPIEL-BARCZYK (1977); echinoids after  
 MACZYŃSKA (1977), except of *Schizaster karreri*

	Korytnica	Chomentów	
		marly sands	red-algal limestones
<b>PORIFERA</b>			
<i>Cliona celata</i> Grant	+	+	+
<i>Cliona vastifica</i> Hancock	+	+	+
<b>POLYCHAETIA</b>			
<i>Serpula</i> sp.	+	+	+
<i>Ditrupa cornea</i> (Linnaeus)	+	+	+
<i>Polydora ciliata</i> (Johnston)	+	+	+
<i>Polydora hoplura</i> (Claparède)	+	+	+
<i>Potamilla reniformis</i> (O.F. Müller)			+
<b>BRYOZOA</b>			
	+	+	+!
<b>BRACHIOPODA</b>			
<i>Lingula demortieri</i> Nyst	+!	+	
<i>Terebratula styriaca</i> Dreger	+	+	+
<b>DECAPODA</b>			
<i>Ocyropsis</i> sp.		+	
Decapoda sp. div.	+	+	+!
<b>CIRRIPEDIA</b>			
<i>Balanus</i> sp. div.	+	+	+
<i>Scalpellum</i> sp.	+		
<b>ECHINOIDEA</b>			
<i>Parasalenia fontanesi</i> Cotteau	+	+	+!
<i>Arbacina</i> sp.	+	+	+
<i>Cidaris</i> sp.			+
<i>Echinocyamus pusillus</i> (O.F. Müller)	+	+	
<i>E. pseudopusillus</i> Cotteau	+	+	
<i>E. circularis</i> Capeder	+	+	+
<i>E. linearis</i> Capeder	+!	+	+
<i>Schizaster karreri</i> Laube	+!	+	+
<b>ASTEROIDEA</b>			
<i>Astropecten</i> sp.	+!	+	+
<b>ELASMOBRANCHII</b>			
<i>Dasyatis</i> sp.	+		
<i>Myliobatis</i> and/or <i>Rhinoptera</i> sp.	+		
<i>Carcharhinus priscus</i> (Agassiz)	+!		
<i>Odontaspis acutissima</i> Agassiz	+		
<b>PELEOSTEI</b>			
<i>Dentex</i> sp.	+!		
<i>Sargus jomnitanus</i> Valenciennes	+		
Vertebrae and bone fragments	+!		

which is considered as a stabilized marine ecosystem, rich in food resources (HOFFMAN 1977). The ecological structure of the *Acanthocardia* assemblage is

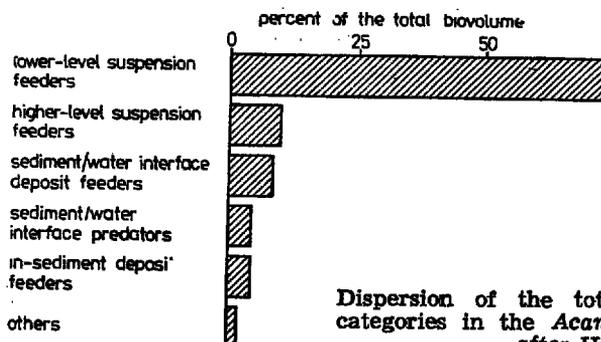


Fig. 5

Dispersion of the total biovolume among trophic categories in the *Acanthocardia* assemblage (scheme after HOFFMAN 1977)

characterized by very high biovolume dominance, whereas within the *Turboella-Loripes* assemblage many feeding and adaptative groups played an equal role, and very low biodominance is observed.

#### ENVIRONMENTAL CONDITIONS

The infaunal suspension feeders dominance may evidence an ecological immaturity of the community (see the *Glossus* assemblage in: HOFFMAN & SZUBZDA 1976). In the case of the *Acanthocardia* assemblage, the interspecific relationships in which are relatively well developed (see Text-figs 6 and 9), the lower-level suspension feeders dominance seems to be rather formed by the abundance of organic matter just above the sediment/water interface (cf. WALKER & BAM-BACH 1974).

The other reason of the high biovolume dominance may be indicated in an environmental stress favoring the species with definite adaptative abilities. The presence of echinoids and asteroids, being one of the essential parts of the assemblage, excludes the oscillations of salinity. When analysing the escape potential (STANLEY 1970), it must be inferred that high hydrodynamic activity was a main factor decisive for the ecological structure of the community. By turn, high energy of water involved the instability of loose sandy bottom. The infauna was, therefore, dominated (see Text-fig. 7) by such very rapid burrowers as *Acanthocardia*, *Paphia*, *Cardium*. Mediate rapid burrowers as *Venus* and *Pelecypora* lived deeper in the sediment in space (cf. DAVITASHVILI & MERKLIN 1966, STANLEY 1970). Young individuals of *Panopea* burrowed very rapidly but adult were slow burrowers. However, adult *Panopea* lived about 1 m below the sediment/water interface and possibility of washing out of the animal from the deposit was very low (cf. DAVITASHVILI & MERKLIN 1966). The schizasterids here were also rapid and deep burrowers.

Within the infauna, a high competition for space is observed (Text-fig. 7). The three of dominating infaunal taxa occupied the three different ecological niches (cf. WALKER 1972): *Acanthocardia* lived just below sediment/water interface, *Panopea* deeply in the sediment, and *Paphia* at the intermediate depths.

A single member of the sessile epifauna, the large oyster *Crassostrea gryphoides* (SCHLOTHEIM), created shell clusters on the bottom surface (see Pl. 3, Fig. 1). Among the pectinids, there appear only free-living forms and a lack of endobysate forms is pronounced.

trophic categories	food resource	infauna		epifauna	
		sessile	vagile	sessile	vagile
suspension feeders	high in water mass			Pectinidae	•Crassostrea
	low in water mass	•Acanthocardia •Panopea •Paphia •Codium •Palaemon •Venus			
deposit feeders	sediment/water interface			•Heterostegina	
	in sediment	Schizaster Nucula			
browsers	sediment/water interface			regular echinoids	
predators	in water mass				
	sediment/water interface			Astropecten	
	in sediment	Natica			
scavengers	carrion	Nassa		crabs	
parasites	host			Scala	

Fig. 6. Trophic-substrate-mobility niches of the *Acanthocardia* assemblage (scheme after HOFFMAN 1977)

Cross-hatched blocks indicate niches not occupied normally by marine benthic animals; taxa marked by black circles indicate members of the trophic nucleus

The browsers are represented by regular echinoids which set up only about 0.1% of the total biovolume. They fed probably on red algae. From the absence of browsing gastropods a lack of seagrasses can be inferred. The unstable bottom of the *Heterostegina* sands has not been accessible for this kind of plant vegetation which consisted only of red algae.

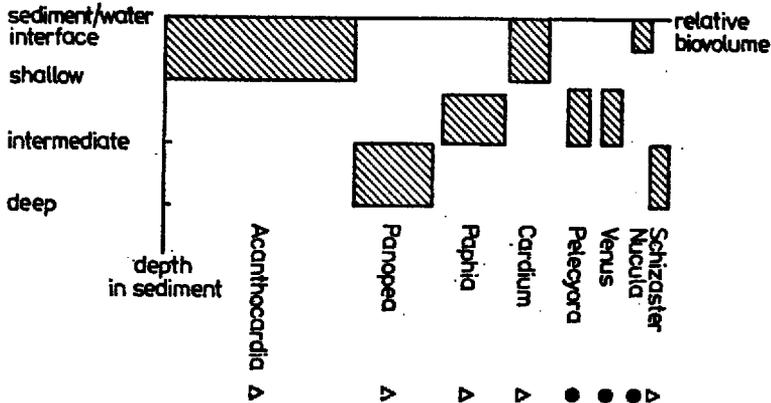


Fig. 7. Spatial relations among the infauna in the *Acanthocardia* assemblage. Indicated are rapid (triangle) and moderate (black point) burrowers (scheme after HOFFMAN 1977).

The abundance of large foraminifers *Amphistegina* and *Heterostegina*, and high energy of the sedimentary environment suggest the depth of deposition about 10 m.

The tropical and/or subtropical climatic conditions prevailing during the deposition of the marly sands as well as the red-algal limestones were recognized earlier (BAŁUK & RADWAŃSKI 1977).

#### TROPHIC WEB

A trophic structure of the *Acanthocardia* community (Text-fig. 8) was very simple (cf. HOFFMAN & SZUBZDA 1976, HOFFMAN 1977). Actually, it consisted mainly of the suspension feeders subweb. The deposit feeders played only minor role in the energy flow, whereas the browsers food chain was very weakly marked.

A more detailed reconstruction of the trophic structure (Text-fig. 9) demonstrates predator competition for food. The naticids, as very active infaunal predators, fed upon infaunal suspension feeders, mainly *Paphia*, *Venus*, *Pelecypora* and *Turritella* (see HOFFMAN & al. 1974). The cassidid gastropods fed upon schizasterid echinoids, which were the main deposit feeders (cf. HOFFMAN 1977). The epifaunal gastropods of the genus *Triton* fed upon semi-infaunal bivalves, and asteroids (cf. DAVITASHVILI & MERKLIN 1968). The most significant predators the starfish *Astropecten*, fed upon pectinids, oysters and semi-infaunal cardids.

The polychaetes, oysters, sponges and holothurians made up the main food resource for parasitic gastropods. Among the suspension feeders the competition for food can be buffered by their space relations of their food resource, i. e. higher-level suspension feeders (oysters, pectinids) and lower-level suspension feeders (see Text-fig. 6).

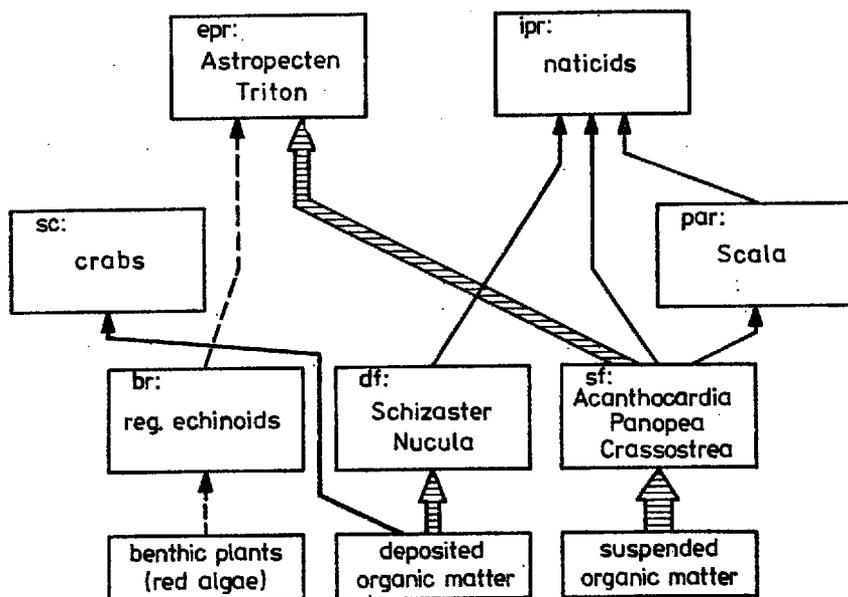


Fig. 8. Simplified trophic web of the *Acanthocardia* assemblage (scheme after HOFFMAN & al. 1978)

Width of the arrows indicates relative significance of the paths  
 br browsers, df deposit feeders, sf suspension feeders, sc scavengers, par parasites,  
 epr epifaunal predators, ipr infaunal predators

Food resource space competition is also recognizable within the deposit feeders group. The benthic foraminifers (*Heterostegina* including) lived on or just below the bottom surface, *Nucula* fed at the depth of several centimeters, and the schizasterids deeply in the sediment (cf. Text-fig. 6).

The plankton feeding fish formed an independent trophic web, the other fishes were probably the predators in the suspension feeders subweb. These two groups were eaten by the carnivorous fish, among which the sharks occupied the highest trophic position.

#### REMARKS ON THE ASSEMBLAGES FROM CHOMENTÓW

Taxonomic composition of the assemblage yielded by marly sands of the lower part of the Chomentów sequence (locality 2 in Text-fig. 1; see also Text-fig. 2B, and RADWAŃSKI 1969, 1970, 1977) demonstrates many analogies to the *Acanthocardia* assemblage from Korytnica (see Tables 1—2). It regards the composition of foraminifer and ostracode association, and the state of preservation of the fossils. The large bivalves *Atrina radwanski* JAKUBOWSKI and *Panopea menardi* (DESHAYES) were found in their life position (JAKUBOWSKI 1977, RADWAŃSKI 1977).

In comparison with the assemblage from Korytnica, the large oysters *Crassostrea gryphoides* (SCHLOTHEIM) are more abundant, and the young individuals dominate what suggests high mortality within the population, caused probably by high water turbulence of this very shallow environment. In such a case *Crassostrea gryphoides* was distinctly *r*-selected.

Of special interest in marly sands are large U-shaped burrows attributable (RADWAŃSKI 1977) to the present-day ghost-crab *Ocypode*. Recently, a large (two meters long) vertical, branched burrow has also been found. This burrow is 4–6 cm and the main inner tunnel 1.5–2 cm in diameter (Pl. 2, Fig. 1); its lateral tunnels being the additional entrances (cf. FREY & MAYOU 1971) are well developed. This burrow reaches the lower erosional surface of the red-algal limestones (Text-fig. 2B).

Taking into account the similarity of taxonomic composition and the role of separate trophic categories between the Chomentów marly sands assemblage and the *Acanthocardia* assemblage from Korytnica, it seems that these two assemblages demonstrate really two different states of the same ecosystem. These states resulted from elastic reactions of the ecosystem developing under local environmental conditions (see HOFFMAN 1979, with references).

In the limestones overlying the marly sands (unit 5 in Text-fig. 2B; cf. RADWAŃSKI 1969, 1977), except rhodoids, the pectinid shell detritus, crab jaws and bryozoans appear abundantly (see Tables 1–2). Among the foraminifers, the heterosteginids, amphisteginids, elphidiids, anomalinids and cibicids are present. The moulds of original aragonite shells occur rarely, and are represented mostly by those of herbivorous trochid gastropods.

The presence mainly of calcite skeletal material, being synsedimentary selected, suggests an impoverishment of the fossil assemblage in comparison with the community which has settled in the red-algal banks. The latter areas are thought to have been occupied by a community dominated by browser trochid gastropods and regular echinoids (see Tables 1–2). Infauna played here minor role, because the loose red-algal, detrital deposit was a poor food resource for deposit feeders, whereas the infaunal suspension feeders were probably unable to burrow in such a sediment. Moreover, the in space was unaccessible because the red-algal crusts could cementate the sediment surface.

Foraminifers of the genus *Heterostegina* appearing within the red-algal limestones are smaller in comparison with those found in marly sands and have thicker tests. Such features may be considered as a result of lower salinity (cf. WALKIEWICZ 1975). In the discussed environment where many echinoderms existed (see Table 2), another reason must however be taken into account.

#### ECOLOGICAL SUCCESSION

In the relatively short time of deposition of the marly sands and red-algal limestones, the temporal and space fluctuation of ecosystem was characterized by elastic reactions under temporary or locally changing environmental conditions (cf. HOFFMAN 1979). The changes of taxonomic composition cannot be considered as short term ecological succession (*sensu* ODUM 1971, PIANKA 1974) because it is impossible to study biologic aspects of the oscillation. The fluctuation of the communities is always connected with the facies development. For example,

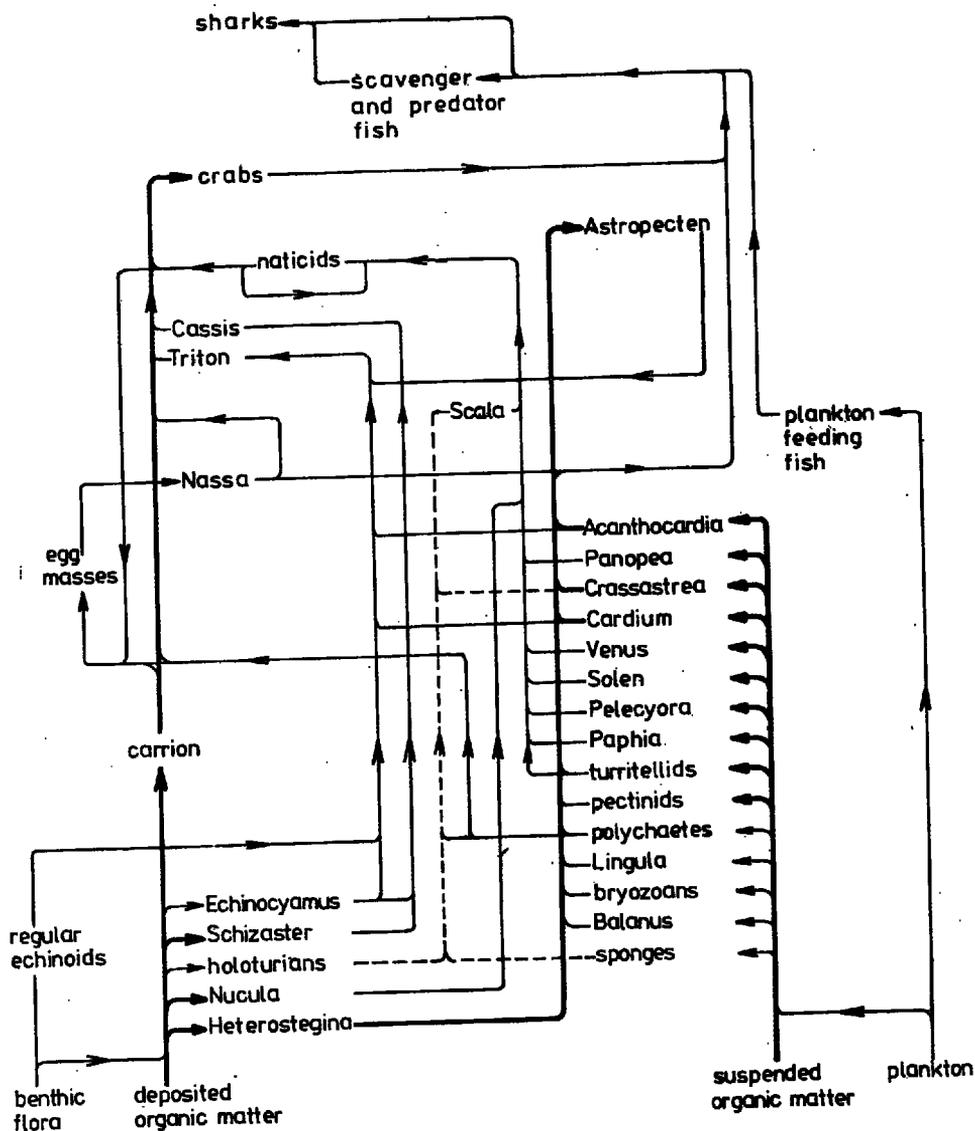
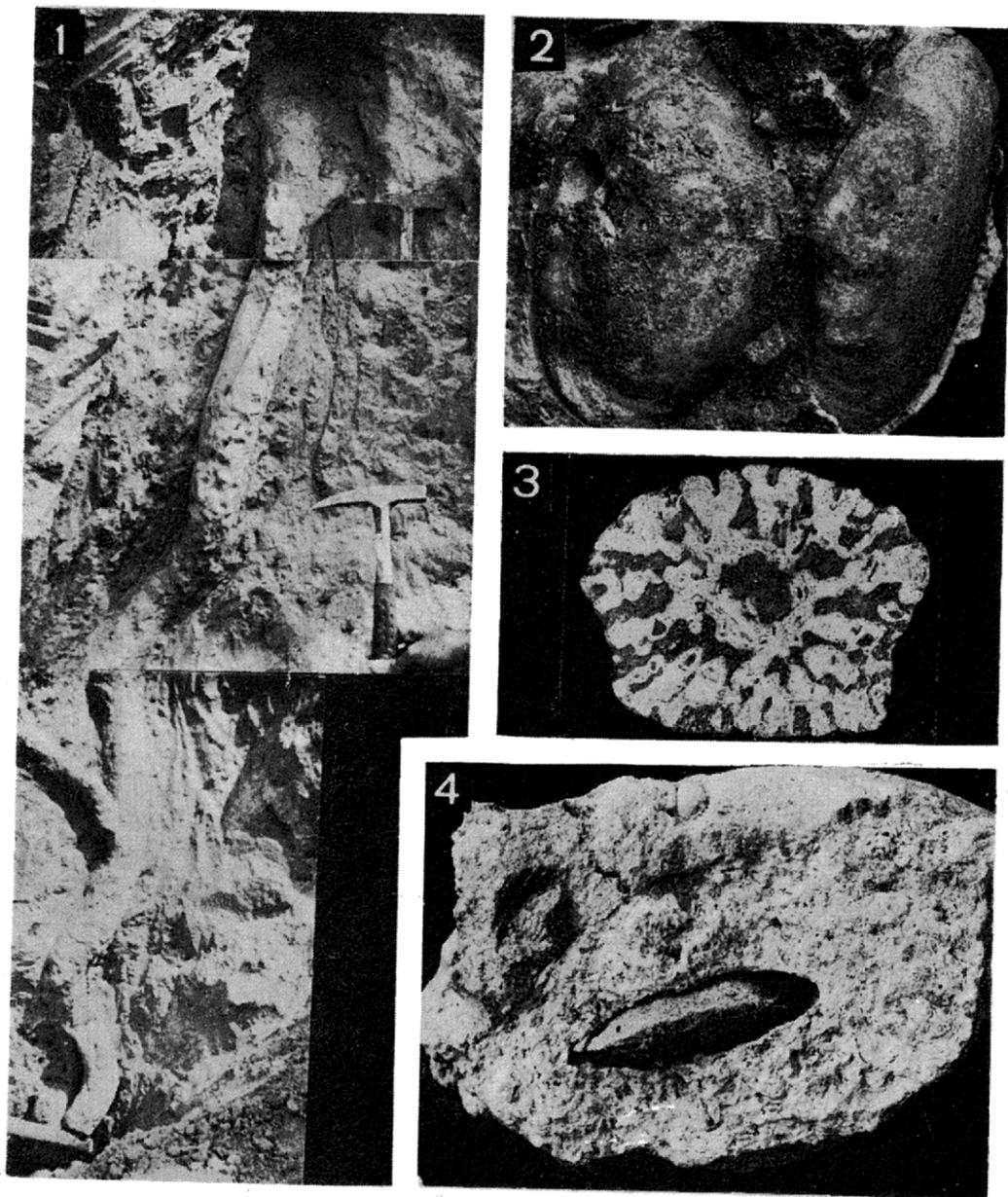
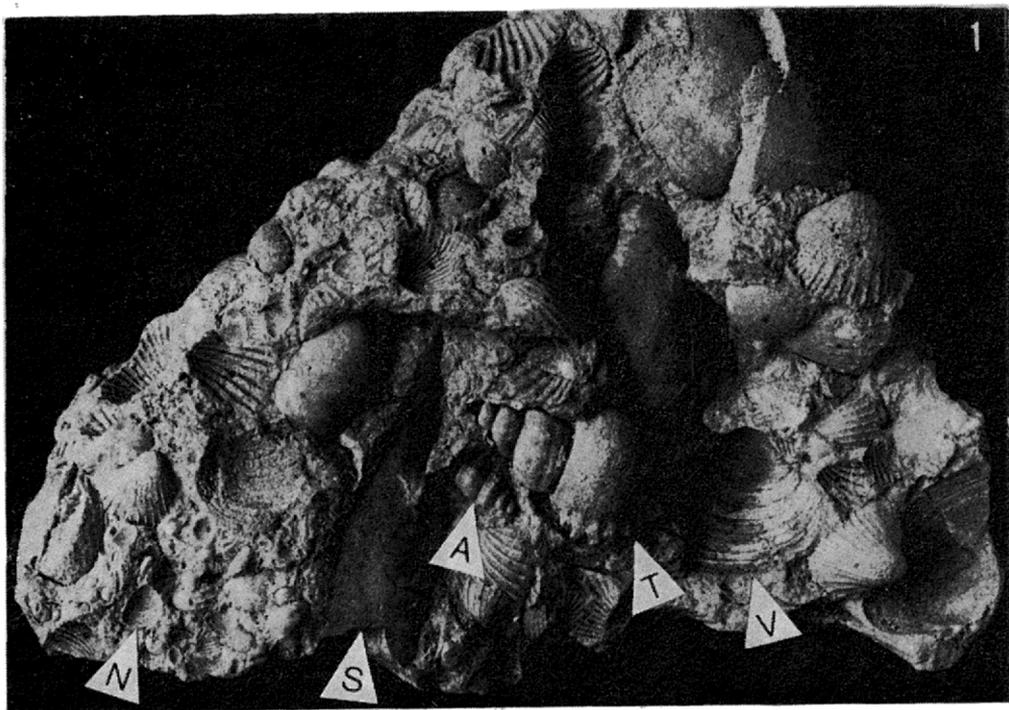


Fig. 9. More complete trophic web of the *Acanthocardia* assemblage (scheme after HOFFMAN 1977)  
 Width of the arrows indicates relative significance of the paths, broken lines indicate inferred members of the community

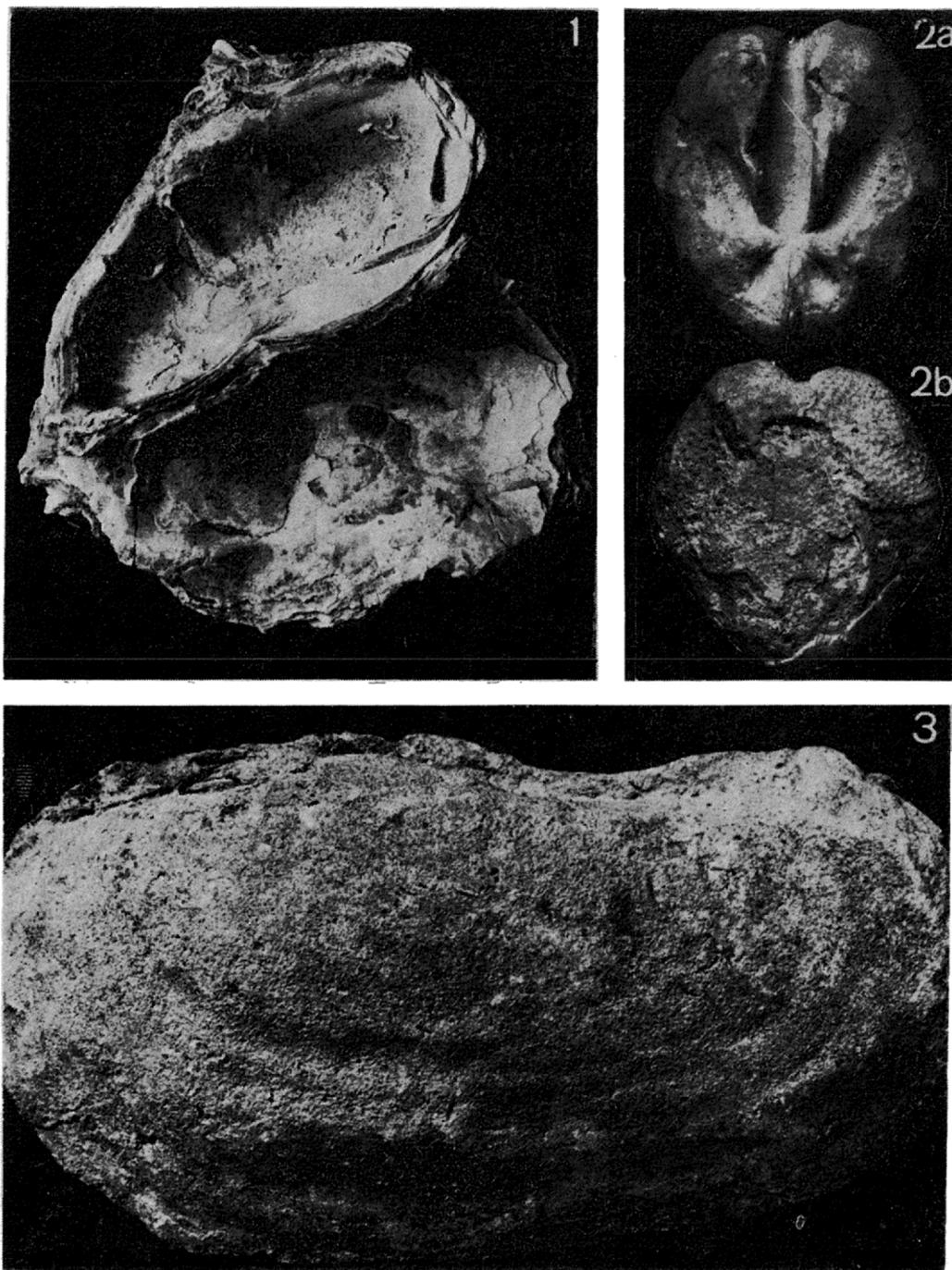


- 1 — An extremely long burrow attributable to the ghost-crab *Ocypode*; Chomentów (unit 3 in Text-fig. 2B)
- 2 — Shell of *Paphia vetula* (BASTEROT) with opened valves; Korytnica (unit 5 in Text-fig. 2A), nat. size
- 3 — Section of an open-branched rhodoid; Korytnica (unit 5 in Text-fig. 2A), nat. size
- 4 — Section of a rhodoid, to show the corallines encrusting a bivalve shell; Korytnica (unit 5 in Text-fig. 2A), nat size



Accumulations of organic remains in marly sands exposed at Korytnica (unit 5 in Text-fig. 2A)

- 1 — Accumulation composed of: N — *Nucula* sp., S — *Solen* sp., A — *Aporrhais pcepelecani* (LAMARCK), T — *Triton affine* DESHAYES, V — *Venus multilamella* LAMARCK, associated with *Acanthocardia paucicostata* (SOWERBY) and *Paphia vetula* (BASTEROT);  $\times 0.75$
- 2 — Mass-accumulation of *Acanthocardia paucicostata* (SOWERBY) and *Paphia vetula* (BASTEROT) associated with rhodoids (arrowed); T — turrillid shell as a nucleus of the rhodoid;  $\times 0.5$



Fauna from marly sands exposed at Korytnica (unit 5 in Text-fig. 2A)

- 1 — Cluster of cysters *Crassostrea gryphoides* (SCHLOTHEIM), with some encrusting serpulids; nat. size
- 2 — Echinoid *Schizaster karreri* LAUBE: 2a aboral, 2b oral view; nat. size
- 3 — Bivalve *Panopea menardi* (DESHAYES); nat. size

the assemblage of the marly sands facies passes into red-algal limestone assemblage (see Text-fig. 2B). Thus, it may be inferred that ecological succession *sensu stricto* has developed too rapidly in the geological time, so this fluctuation cannot be observed in the sedimentary sequence.

The *Acanthocardia* assemblage, typical of the marly sands, is well developed just above the Korytnica Clays containing their own fauna (see BAŁUK & RADWAŃSKI 1977, 1979; HOFFMAN 1977, 1979). However, the density of fossil assemblage in the lower part of the sequence is low. The *Acanthocardia* assemblage reaches its maturity within the *Heterostegina* sands (unit 5 in Text-fig. 2A). Both the diversity and density of the assemblage, adapted to a bottom mobility are here the highest.

Intercalations of coherent marls and marly sandstones within the topmost part of the Korytnica Clays are the first record of the storm events in the Basin. The *Acanthocardia* assemblage which colonized the sandy bottom above the clays can be treated, therefore, as the post-event community *sensu* SEILACHER (1982). Within the overlying members (except unit 6 in Text-fig. 2A) the fossil assemblage did not change because several event deposits are granulometrically undistinguishable from the background.

At the top of the sequence (unit 6 in Text-fig. 2A), diversity of the assemblage decreases. The fossil assemblage is strongly dominated by *r*-selected *Turritella* sp., adapted to the conditions of low sedimentation rate and of more stable bottom which have been recognized for sandy-glaucopitic red-algal limestone deposition (GUTOWSKI 1983).

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**ŚRODOWISKO SEDYMENTACJI I SYNEKOLOGIA ZESPOŁÓW  
MAKROBENTONICZNYCH PIASKÓW MARGLISTYCH I WAPIENI  
LITOTAMNIOWYCH BASENU KORYTNICY**

(Streszczenie)

Głównymi czynnikami kształtującymi środowisko sedymentacji osadów przykrywających ily korytnickie były wysoka aktywność czynników hydrodynamicznych oraz zróżnicowana batymetria. W pobliżu podwodnych, skalistych grzbietów rozwinęła się facja wapieni glonowych, zaś w nieco głębszej, środkowej części basenu osadzone były piaski margliste (patrz fig. 1—3). Analiza synekologiczna makrobentonicznego zespołu *Acanthocardia* z piasków marglistych (patrz fig. 4—9, tab. 1—2 oraz pl. 1—3) wykazała, że zespół zdominowany był przez małże żywiące się zawieszoną z toni wodnej. Jeden gatunek, *Acanthocardia paucicostata* (SOWERBY), stanowił ok. 34% całkowitej bioobjętości zespołu. Wśród organizmów infaunistycznych przeważały szybko zagrzebujące się małże dostosowane do wysokoenergetycznego, niestabilnego środowiska. Zespół stowarzyszony z łachami glonowymi składał się głównie z epifauny bądź roślinożernej (ang. *browsers*), bądź żywiącej się z zawiesziny (ang. *suspension feeders*). Zarówno wskaźniki sedymentologiczne jak i ekologiczne sugerują sztormowy charakter badanej sekwencji osadów w całym Basenie Korytnicy.

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