acta
geologica
polonica

Vol. 27, No. 2 Warszawa 1977

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Synecology of macrobenthic assemblages of the Korytnica Clays (Middle Miocene; Holy Cross Mountains, Poland)

ABSTRACT: The distribution patterns of forty dominant taxa (lithothamnia and macrobenthic animals) of the Korytnica Clays (Middle Miocene; Holy Cross Mountains, Central Poland) are used to analyse the structure of paleoecosystem. Q-mode factor analysis of correspondences allows to distinguish six assemblages, viz. (1) *Turboella-Loripes*, (2) *Corbula*, (3) *Corbula*-spatangoid, (4) turritellid, (5) *Pteromeris*-coral, and (6) *Ostrea* assemblages. R-mode factor analysis of correspondences allows to recognize in detail the environmental control of these assemblages. The macrobenthos of the Korytnica basin was controlled mainly by water turbidity, presence of the seagrasses, variability of bottom microrelief, water turbulence, and oxygen capacity in nearbottom layers. The ecological structure of assemblages is described in terms of their taxonomic composition and diversity, trophic structure, and spatial structure of the infauna. The order of ecological succesion leading from pioneer colonization of a barren muddy substrate to development of a mature seagrass community is reconstructed. The assemblages are also compared to their present-day and ancient counterparts. The obtained results have served to test but fail to corroborate some common ecological hypotheses relating ecological complexity, taxonomic diversity, ecological maturity, and environmental predictability to each other.

INTRODUCTION

The world-famous Korytnica Clays (Middle Miocene) developed on the southern slopes of the Holy Cross Mountains, Central Poland, are well known to contain abundant and excellently preserved fauna (*cf.* Bałuk & Radwański 1977). As the matter of fact, the fossil assemblage is among the richest and most diverse assemblages of the European Neogene. It consists mainly of mollusks which are accompanied by a nearly complete set of other marine benthic invertebrates and by some fish. The paleogeographical situation of the Korytnica basin is so well recognized (*cf.* Bałuk & Radwański 1977) that the Korytnica Clays appear to be ideally suited for paleoecological studies.

This study deals with the structure of the Korytnica paleoecosystem. It is an outgrowth of a combined autecologic and synecologic analysis of the macrobenthos. In addition, the informations available on nektic, planktic, and microbenthic members of the ecosystem have also been considered. The comparative studies with Recent as well as ancient communities have been undertaken, in order to better understand the environmental and biological controls upon the Korytnica macrobenthic assemblages.

This study is also intended to provide the data necessary for testing and further evaluation of evolutionary-ecology models, that is to enable an insight into complex relationships between the structure and evolutionary behavior of a community and those of its constituent populations. In fact, when the biotic evolution is regarded as a process governed by the higher-order ecological organization, it is necessary to study not only populations and their evolutionary development through geological time, but also to solve the decisive problems found in the organization and order unifying them into communities.

Acknowledgements. This paper makes part of doctoral thesis submitted to the University of Warsaw, and supervised by Docent A. Radwański to whom the author expresses his most sincere thanks. The author is also deeply grateful to Docent W. Bałuk and Dr. G. Jakubowski for making available their paleontological collections and preliminary taxonomic comments. Dr. J. F. Cottrell has kindly supplied a copy of his unpublished work on seagrass root etchings. The author has highly benefited from the numerous discussions with M. Narkiewicz, A. Pisera, M. Ryszkiewicz, W. Studencki, and B. Szubzda-Studencka. Some of the ideas considered in this paper were also more or less thoroughly discussed with Dr. P. W. Bretsky, Dr. F. T. Fürsich, Dr. R. J. Stanton, and Dr. K. R. Walker.

GEOLOGICAL SETTING

The Korytnica Clays were deposited in a small basin in the terminal part of the Korytnica Bay formed when the Middle Miocene (Badenian) sea transgressed onto the southern slopes of the Holy Cross Mountains (Radwański 1969, 1974; *cf.* also Bałuk & Radwański 1977). The separation of the Korytnica basin from the rest of the Korytnica Bay was due to pre-Miocene morphology; in fact, the basin appears to have represented a drowned valley, the slopes of which were formed by the Jurassic limestones, delimiting the shoreline (Fig. 1).

The facies development of the Korytnica basin was recognized by Radwański (1969), and it may be briefly summarized as follows: Entering the valley, the Middle Miocene (Badenian) sea came upon the waste deposits which gave the origin to the brown-coal bearing sediments and quartz sands underlying the Korytnica Clays. The Korytnica Clays represent a monotonous, 40—60 m thick set of cream-colored, yellow to almost white, marly silts and clays with an appreciable proportion of sand-sized particles. Locally, an oyster shell-

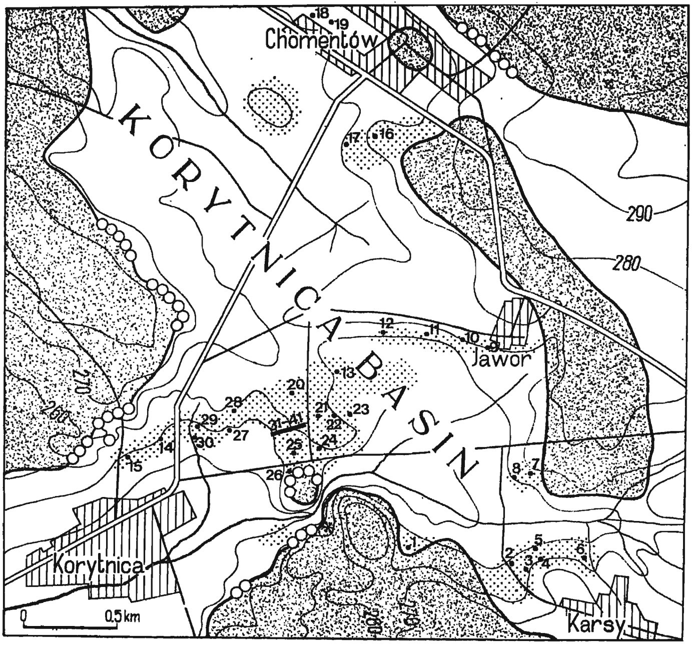


Fig. 1. Paleoenvironmental sketch of the Korytnica basin (*from:* Bałuk & Radwański 1977, Text-fig. 2)

Indicated are: marine area of the Korytnica basin during the Middle Miocene (Badenian) transgression *(blank)* and present-day outcrops of the Korytnica Clays *(stippled)*; preserved fragments of littoral structures *(circled)*; land or island areas along the seashore *(hachured)*
Numbered are sampling places *(1—41)* for the investigated macrobenthic assemblages

bed occurs as a littoral facies. General ecological characteristics of organic communities of the Korytnica Clays indicate a successive decrease in depth due to a gradual filling of the basin up with the accumulating deposits. The Korytnica Clays are overlaid by fine-grained marly sands deposited in a very shallow environment. Locally, red-algal (lithothamnian) limestones appear as the uppermost part of the sequence.

METHODS

In this study Parker's (1975) notion of marine benthic community as an actual association of populations, controlled by continuously interplaying extrinsic and intrinsic factors, is accepted. In fact, this concept appears also entirely consistent with the holistic approach suggested recently by Kauffman & Scott (1976).

However, the term *fossil assemblage* will be used rather than *community,* when considering the empirical distribution patterns. As the matter of fact, the former term is a more descriptive one and its use may emphasize that because of sampling limitations and information losses one deals with a small and biased sample of the original community (*cf.* Johnson 1964; Lawrence 1968, 1971; Stanton 1976). The use of the term *community* will be restricted to design original associations of living organisms.

As noted by Speden (1966), the recognition of paleocommunities by distinctive associations of organisms is more subtle than that by a physical parameter. Therefore, the relative-abundance data on distribution of the Korytnica dominant taxa were studied by means of both Q-mode and R-mode factor analyses of correspondences (program *TABET-1*; Benzecri 1973). This particular method of factor analysis was chosen because it allows the use of continuously changing variables together with discontinuous and arbitrarily coded ones. Parks (1966) and Park (1974) postulated than in order to remove redundancy in data, R-mode analysis should be performed before the Q-mode classification is undertaken. However, in the case of this method, redundancy is eliminated by the algorithm itself. Hence, the Q-mode classification of the samples into discrete classes (that is fossil assemblages) was performed at first.

In each of the samples the abundances of dominant taxa had to have been determined. In the case of all mollusk taxa and *Ditrupa cornea*, this was accomplished by their representation as percent proportions of the total number of macrobenthic individuals in a given sample. These data were obviously biased by differential mortality patterns and escape potentials among the taxa. Nevertheless, it can be postulated that normally these two aberrations affect all samples within an ecosystem equally. In the case of the lithothamnia, solitary corals, bryozoans, and spatangoids, the abundance in each of the samples was determined approximately and coded arbitrarily.

A procedure converting the absolute-abundance data into percentage relative-abundance data may result in spurious correlations and thus, obscure the true interrelationships among the variables. However, in the factor analysis of correspondences the association among variables is measured by means of a weighed distance in multidimensional Euclidean space. Therefore, if all the samples are to be regarded as equally important, the effects of their differential size must be eliminated from the analysis (*cf.* David & *al.* 1974).

The R-mode factor analysis was used to facilitate the environmental interpretation of the habitats settled by the distinguished fossil assemblages. Therefore, autecology of the dominant taxa must have been assessed at first. In this study all autecological interpretations are based on informations about living organisms that can be regarded as conspecific with the Miocene species discussed or at least as belonging to closely related species; in several cases, inferences from shell morphology were also taken into account (Hoffman 1976a). Feeding types of the benthic taxa are categorized accordingly to the recent discussion and classification by Walker & Bambach (1974). One should, however, keep in mind that many species cannot be ultimately ascribed to one feeding category or another because of their distinct behavioral switch mechanisms. Nevertheless, for the purposes of this study such a simplified classification seems adequate.

At last, the ecological structures of the Korytnica macrobenthic assemblages were analysed in detail and compared to their extant and extinct analogues. Ecological structure of a community is here meant as the whole of trophic and other biological interrelations among all community members, and of their autecological relations to the abiotic environment. Thus, a basic characteristics of an ecological structure should always involve several autecological analyses as well as more or less detailed analyses of taxonomic, trophic, and spatial structures of the community.

The autecological analyses of the Korytnica dominant taxa are presented separately (Hoffman & *al.* 1974; Hoffman 1976a, b, c). Therefore, only synecological analyses will be given in this paper. In fact, any statistically significant differences in morphology or population dynamics have not been found among the conspecific mollusk populations from within different fossil assemblages.

The Korytnica basin appears to have been too small and homogeneous to allow spatial separation of genetically distinct macrobenthic subpopulations. This confirms the validity of an approach extending the autecological interpretations over all samples of the Korytnica Clays.

The above approach is, however, justified in paleoecological research only when there is evidence that nearly all the specimens belonged to the same ecological community and are present in about the same size and numbers as when they were alive. In the Korytnica Clays a minimum of post-mortem alteration is evidenced by the ecological coherence of assemblages found in the samples, the unique discrete distribution patterns of particular benthic species, the similar preservation state of all specimens, the preservation of even very thin and fragile shells, the extreme diversification of shapes and modal values of size-frequency histograms, and nearly the same abundance of the opposite valves of bivalve shells; the overall homogeneity of fine-grained sediment, and the paleogeographical situation of a closed and shallow basin strongly support the inference about the lack of any significant post-mortem sorting or transportation (*cf.* Johnson 1960; Fagerstrom 1964; Scott 1970, 1974; Lasker 1976). Although shell fragments are relatively abundant, the more or less random distribution of the fractures which are not restricted to the most thin parts of the shells, and their generally sharp edges may suggest that they resulted primarily from compaction crushing. Some bias can, however, be introduced into the data by selective breakage resulting from the activities of certain scavengers or predators, such as the pagurid crabs or fish. Any traces of chemical corrosion are not evidenced within the skeletal remains, which may indicate total lack of skeletal-carbonate, aragonite including, dissolution.

MATERIALS

An ecological community can be characterized by a group of diagnostic species which are common in samples from within the community. Nevertheless, because of a clearly polythetic (*sensu* Sokal & Sneath 1963) nature of benthic communities, none of these species is present in every sample, and none of these samples contains all diagnostic species (Valentine 1973). Therefore, the ability to recognize benthic communities is determined by the number and size of samples available. As shown by Stanton & Evans (1972), the sample size necessary to define or recognize a community is also strongly influenced by structural characteristics of the community.

Hence, forty one bulk samples (*cf.* Fig. 1), each of 2—3 kg of the deposit, were washed by a mesh screen of 0.45 mm, and all recognizable skeletal remains (more than 25,000 specimens) were collected. In addition, two bulk samples, each of more than 100 kg, were analysed as well as the paleontological collections made available by Docent W. Bałuk and Dr. G. Jakubowski. Thus, the materials enable analysis of very fine distributional patterns and consequently, of subtle ecological relationships. However, in the Korytnica Clays one cannot determine any strictly isochronous surface. Hence, the results of the present study will not allow to present any precise paleoecological map but only to recognize somewhat abstract, general spatial relations in the Korytnica basin, and interrelationships between the fossil species and their biotic and abiotic environment.

RECOGNITION OF FOSSIL ASSEMBLAGES

In order to recognize the fossil assemblages, that is to partition the sample set into discrete classes, the unnormalized relative-abundance data were studied by means of Q-mode factor analysis (Tab. 1). The first seven factor axes account

Table 1

Q-mode factor analysis of distribution of the Korytnica dominant taxa; for location of the samples *see* Text-fig. 1

Sample	I axis	II axis	III axis	IV axis	V axis	VI axis	VII axis
1	2796	-1342	-748	-1381	195	-72	-135
2	284	-160	161	-260	-310	349	300
3	-169	-166	36	-87	-694	-70	-239
4	-57	212	-110	-66	-33	11	264
5	117	712	-162	31	-68	16	-586
6	-166	82	-136	-35	51	54	356
7	-622	-455	-515	99	464	7	-86
8	-346	-250	-252	58	42	-217	303
9	69	-409	-1345	119	62	-1009	72
10	-649	-604	-444	136	450	-79	-166
11	228	-401	1486	55	12	-832	173
12	-702	-601	-555	138	339	47	-284
13	-413	-329	-104	-20	-632	-51	-280
14	-33	369	7	-241	-750	123	136
15	-232	-221	30	-89	-592	-7	-48
16	88	-509	1740	160	359	314	-327
17	395	1020	65	-161	-60	-148	-147
18	214	-338	1637	-68	314	930	-10
19	-160	-123	-161	-67	154	2	356
20	-378	-236	-277	9	66	12	81
21	283	1213	-102	-9	364	-71	-244
22	-286	-233	40	-46	-670	-29	-209
23	-532	-484	-336	53	43	-26	-169
24	-82	-74	282	-46	-591	238	-140
25	-653	-567	-510	119	246	55	-323
26	2199	-431	-547	2396	-205	104	129
27	-66	176	-2	-95	0	153	537
28	-548	-439	-438	42	-135	83	-316
29	-150	239	-179	-80	7	88	208
30	-478	-351	-369	55	370	31	207
31	365	1285	-78	41	303	-125	-328
32	-384	-283	-252	24	180	7	241
33	333	1170	22	-86	244	-16	17
34	-387	-250	-289	24	204	-28	167
35	-329	-169	-209	0	108	-16	241
36	-298	-83	-236	73	167	-26	-52
37	-446	-353	-285	36	216	-76	111
38	368	1392	-95	16	195	-92	-495
39	271	1235	-118	-35	223	-55	-40
40	126	870	-7	-246	-102	80	520
41	207	933	19	-191	-46	131	362
variability accounted for by the axis	22.9%	19.9%	17.2%	10.1%	5.7%	4.0%	3.6%

for almost 85% of the total variability. Thus, the factor-spatial relations among the samples appear relatively simple and clearly identifiable. However, the parsimony of the factor-analytic solution was not statistically estimated. Only the first five factors will be considered in detail because all the other factors may represent the artifacts of the square-matrix analysis in a closed system of numbers.

The weights of all samples are almost equal (Tab. 2). Nevertheless, the actual influence on the analysis is distinctly different among the samples; this indicates clearly heterogeneity of the sample set. The most important in the analysis are the samples *1* and *26* (cf. Fig. 1). As the matter of fact, the quality of their representation by the analysis is perfect. In general, the quality of sample representation by the analysis is good; only a few samples are underrepresented (Tab. 2). The perfunctory analysis of the factor matrix indicates that most underrepresented samples have high loadings on the seventh factor axis. Therefore, this axis will also be considered in some detail.

When the sample set is considered in the abstract space of first five factors, a few distinct sample classes can easily be recognized (Fig. 2). The

Table 2

Reliability of the Q-mode factor analysis of distribution of the Korytnica dominant taxa

Sample	Actual influence on the analysis	Weight	Quality of representation by the analysis
1	175	28	998
26	132	23	999
16	61	30	904
18	57	28	951
11	41	24	920
9	40	25	939
38	28	21	917
31	25	22	899
19	23	24	113
21	22	22	888
17	22	23	683
5	22	22	468
33	21	24	890
39	21	22	852
40	19	23	711
12	18	23	906
24	18	25	372
25	17	24	847
41	17	24	798
14	17	29	701
10	16	23	895
3	16	30	567
2	15	23	385
8	15	24	312
7	14	23	932
13	14	27	746
28	13	27	846
27	13	24	349
15	12	26	505
22	10	26	862
23	10	24	815
30	9	23	898
32	7	24	689
37	6	24	904
4	6	25	285
34	5	23	804
6	5	23	414
20	4	24	806
35	4	24	771
36	4	23	616
29	4	23	542

remaining 14 samples among which there are most underrepresented samples, appear to be most intimately connected with another fossil assemblage (denoted by black circles in Fig. 2). However, when these two sample classes are analysed jointly on a scattergram of the first axis versus the seventh one, a difference in the loadings on both axes becomes evident (Fig. 3a). Thus, these two sample classes are to be regarded as the subsets of a single fossil assemblage. A similar scattergram of the second axis versus the seventh one allows the distinction between two subsets of another fossil assemblage (Fig. 3b). The fossil assemblages and subassemblages are named after their most dominant macrobenthic constituents (Tab. 3).

The overall taxonomic composition is fairly similar among all the fossil assemblages of the Korytnica Clays. Indeed, presence-absence analysis of the distribution patterns of dominant taxa would show the samples to be almost identical. Nevertheless, each of these taxa exhibits a unique distribution pattern with its own center of abundance (Fig. 4). Some taxa are obviously more or less evenly distributed, whereas others are concentrated in the samples from within a single fossil assemblage.

Evenness of the distribution pattern of a given taxon is measured by its fidelity, that is the extent to which it is confined to a single fossil assemblage. Fidelity is here defined as the ratio of minimum to actual value of the total sum of normalized average relative-abundances of a taxon in all fossil assemblages. The higher is the fidelity of a taxon, the more is this taxon typical of a single fossil assemblage. Therefore, fossil assemblages are most easily distinguished by the use of high-fidelity taxa. The larger is the proportion of high-fidelity taxa, the more distinct is a fossil assemblage. Distinctness of the Korytnica assemblages, and fidelity of the lithothamnia and dominant macrobenthic animals are presented graphically (Fig. 4).

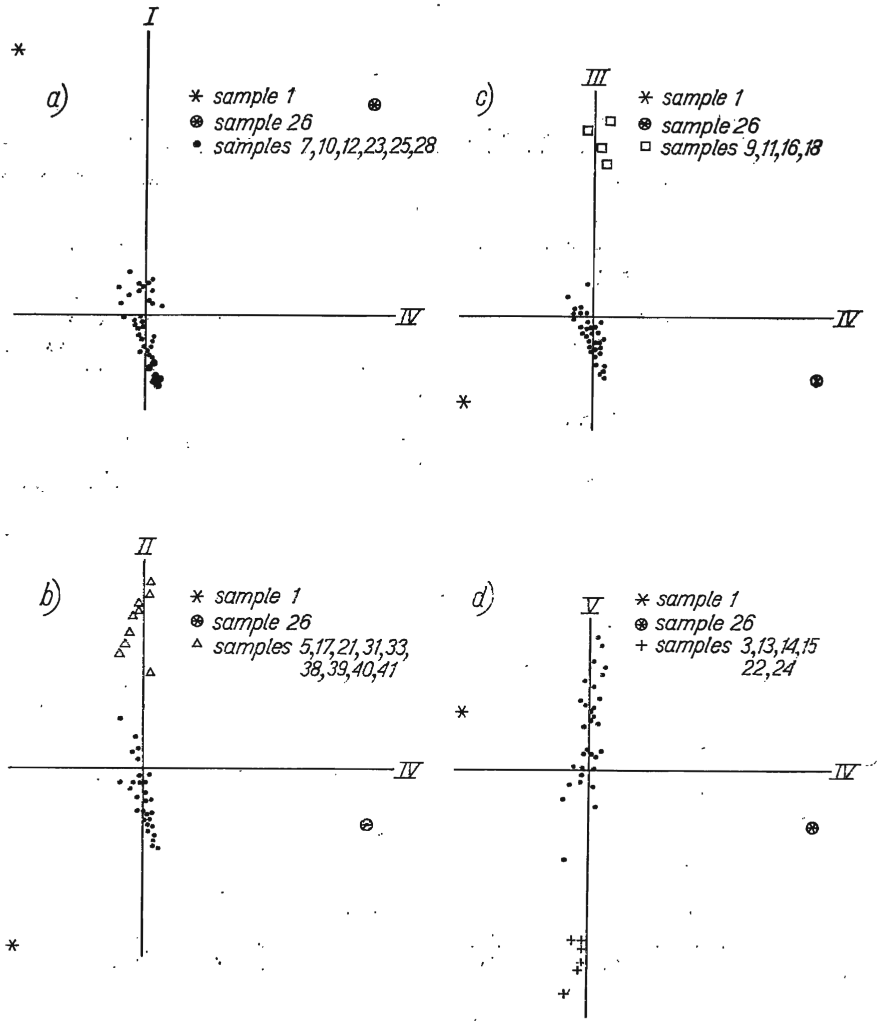


Fig. 2. Q-mode factor analysis of distribution of the Korytnica dominant taxa: scattergrams of the first five factor axes

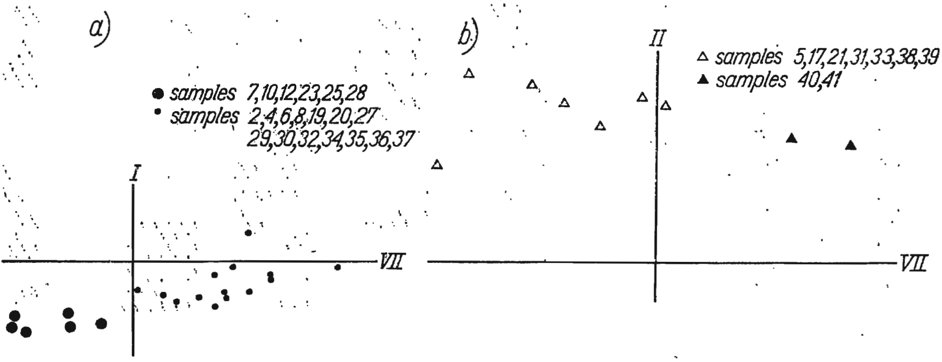


Fig. 3. Q-mode factor analysis of distribution of the Korytnica dominant taxa: additional scattergrams allowing subdivision of two fossil assemblages
a — *Corbula* assemblage, b — *Turboella-Loripes* assemblage

Table 3

Macrobenthic fossil assemblages of the Korytnica Clays

Samples	Fossil assemblages
5, 17, 21, 31, 33, 38, 39	*Turboella-Loripes* subassemblage
40, 41	*Turboella-Loripes*-*Pyrgulina*-scaphopod subassemblage
7, 10, 12, 23, 25, 28	*Corbula* subassemblage
2, 4, 6, 8, 19, 20, 27, 29, 30, 32, 34, 35, 36, 37	*Corbula*-scaphopod subassemblage
3, 13, 14, 15, 22, 24	*Corbula*-spatangoid assemblage
9, 11, 16, 18	turritellid assemblage
1	*Pteromeris*-coral assemblage
26	*Ostrea* assemblage
-	*Neritina*-*Nassa*-*Melanopsis* assemblage

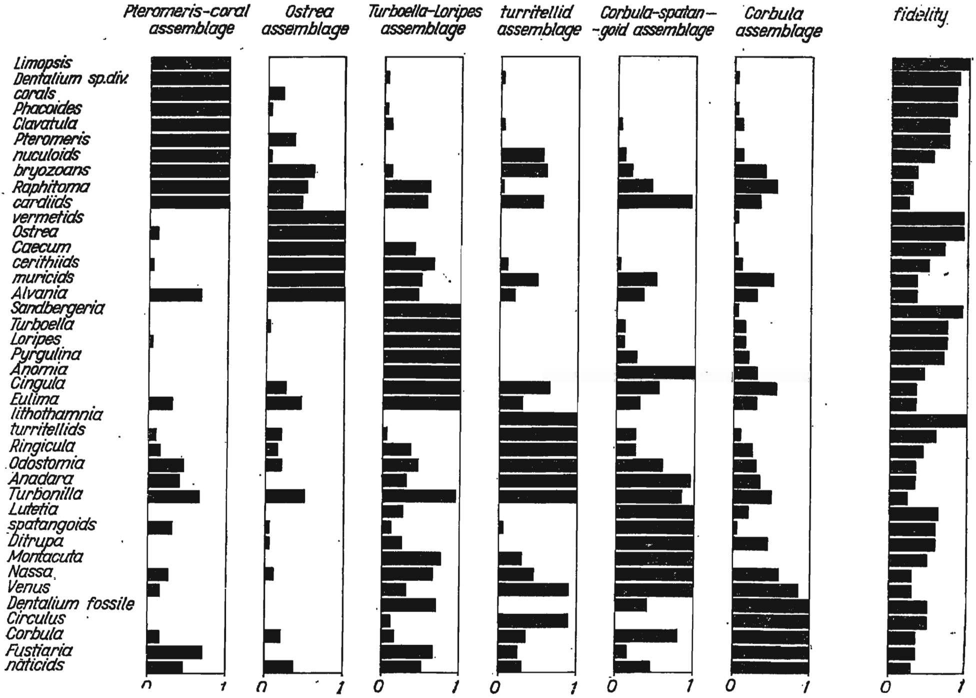


Fig. 4. Averaged distribution patterns of the Korytnica dominant taxa in the recognized assemblages; bar length indicates the proportion of maximum abundance of a taxon

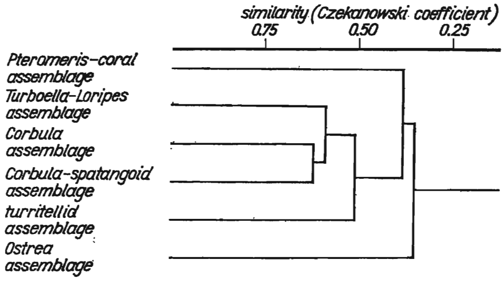


Fig. 5

Similarity dendrogram of average taxonomic composition of the recognized assemblages

The similarity dendrogram among the fossil assemblages (Fig. 5) clearly demonstrates that the *Corbula*-spatangoid and *Corbula* assemblages are very similar to each other. On the other hand, high distinctness of the *Pteromeris*-coral and *Ostrea* assemblages appears related to the apparent difference of these assemblages from the others.

ENVIRONMENTAL CONTROL OF FOSSIL ASSEMBLAGES

Physical-chemical environment is well known to exert important control over the composition and structure of benthic communities. The influence of such abiotic factors as bathymetry, salinity, oxygen capacity, or water temperature has been extensively studied by marine biologists and ecologists, and it may also be easily recognized in the fossil record. However, the geographical situation of the Korytnica basin, and overall taxonomic similarity of benthic fauna among the Korytnica assemblages strongly suggest that any dramatic difference in such environmental parameters is improbable.

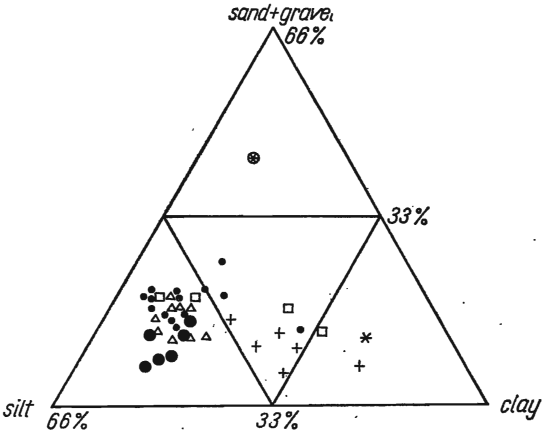


Fig. 6

Percentage of (*1*) sand & gravel, (*2*) silt, and (*3*) clay in the sediment associated with the analysed samples; graphic marks for the recognized assemblages the same as in Text-fig. 2

Substrate type has also been assumed to be among the main ecospace parameters controlling spatial distribution of benthic animals, and it was recently recognized (Bałuk 1972) to have significantly influenced the distribution patterns of Korytnica scaphopods. Therefore, the grain-size images of the associated deposits were determined for all the samples considered.

The substrate is very homogeneous among the majority of the samples. Generally, this is a mud or silty clay (Fig. 6). Only the sample *26* markedly differs from all the others. In fact, it was derived from the oyster shellbed of Korytnica and is considerably enriched in sand-sized or even gravel-sized particles. The ternary sediment-texture diagram demonstrates also that the sample *1* (i.e., the *Pteromeris*-coral assemblage) is associated with a relatively pure clay. High clay content is also typical of the samples from within the *Corbula*--spatangoid assemblage.

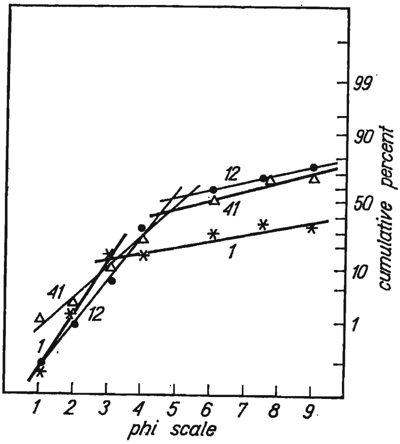


Fig. 7
Grain-size distributions of the sediment associated with selected samples

The probability curves and truncation points of the most typical samples (Fig. 7) indicate clearly that with the exception of the oyster shellbeds, the clays of Korytnica represented originally soft, fine-grained substrate deposited almost entirely from suspension. In fact, the relationship between the values of one--percentile and median of the clay associated with sample *1* suggests that it originated from pelagic suspension (*cf.* Passega & Byramjee 1969). Presumably this sample represents a facies analogous to the modern bay-center muds of Kraft (1971). On the other hand, the majority of samples originated from a combination of uniform suspension and pelagic suspension; weak currents could also contribute to accumulation of the deposit. Then, the samples may represent an environment analogous to that of the bay-margin muds of Kraft (1971).

Thus, the sharp difference between the *Pteromeris*-coral and the other assemblages may, indeed, be controlled, at least in part, by the substrate type. The latter can obviously be also related to some other environmental factors. On the other hand, the overall homogeneity of the deposit indicates that substrate type could not account for the variation in distribution patterns of most dominant taxa.

Insofar, any burrows have not been recorded in the Korytnica Clays. The sediment lacks also any sedimentary structures, which makes impossible direct inferences about nearbottom conditions.

In order to recognize the environmental control of the Korytnica macrobenthos, the relative-abundance data on forty dominant taxa were studied by means of R-mode factor analysis (Tab. 4). The R-mode factor-analytic solution ensured by the algorithm of Benzecri (1973) is entirely analogous to the Q-mode solution of a given data matrix. In other words, the R-mode and Q-mode factor axes derived from a single data matrix are the same. Therefore, the R-mode analysis of the Korytnica samples allows to interpret directly in environmental terms the Q-mode samples classification.

Table 4

R-mode factor analysis of distribution of the Korytnica dominant taxa

Taxon	I axis	II axis	III axis	IV axis	V axis	VI axis	VII axis
lithothamnia	213	-653	2747	110	769	1286	-455
corals	3210	-1453	-955	-1409	197	-52	-146
Ditrupa	-352	-150	-229	-5	-433	237	-346
bryozoans	429	-341	268	-7	14	-113	245
Fustiaria	-40	258	-178	-173	250	-51	673
Dentalium fossile	-54	412	-155	-199	73	11	788
Dentalium sp. div.	2330	-1047	-204	-1742	313	23	-32
nuculoids	854	-711	715	-555	101	-958	141
Anadara	-142	-187	190	-98	-182	-63	292
Limopsis	4160	-2141	-1286	-3097	582	-260	-510
Anomia	-73	561	-189	-143	-590	56	-480
Ostrea	3294	-783	-949	4633	-520	331	408
Loripes	283	1384	-108	-190	197	-51	1
Phacoides	1520	-1016	-465	-1324	-53	115	-20
Montacuta	113	570	242	-272	-1013	-385	-74
Pteromeris	3643	-1649	-1001	-831	253	60	-195
cardiids	291	58	183	-177	-517	394	-340
Lutetia	-272	31	-92	-105	-988	-28	-169
Venus	-218	-102	120	-63	-307	-400	286
Corbula	-499	-416	-341	71	173	-3	-70
Circulus	-19	-133	474	-175	153	758	848
Cingula	94	458	234	-187	-112	404	665
Turboella	264	1336	-133	-92	276	-70	-355
Alvania	428	249	-72	191	-128	133	-101
turritellids	146	-385	1344	145	-41	-570	-33
vermetids	1901	-361	-407	3022	-350	127	358
Caecum	824	1066	-269	888	192	-108	-234
Sandbergeria	354	1684	-138	-70	590	-154	-465
cerithiids	586	1029	-125	509	230	-214	-318
Turbonilla	242	408	308	-120	-142	23	153
Odostomia	236	137	628	-167	-186	495	111
Pyrgulina	221	1291	-59	-284	-107	110	546
Eulima	274	807	46	-63	60	23	153
naticids	-76	45	-170	17	102	71	387
muricids	68	208	-89	296	99	174	361
Nassa	-48	233	61	-146	-262	236	178
Clavatula	1326	-371	-215	-1110	-60	286	198
Raphitoma	264	354	-186	-149	-150	39	277
Ringicula	143	112	649	-57	-55	-412	197
spatangoids	-118	-36	-107	-209	-1033	88	-279
variability accounted for by the axis	22.9%	19.9%	17.2%	10.1%	5.7%	4.0%	3.6%

The weights of the taxa are very diverse (Tab. 5). This was to be expected when taking into account extremely diverse numerical abundances of benthic invertebrates. However, the actual influence of a taxon upon the analysis depends not only on its weight, but also on the variance of its relative abundance in the samples. Therefore, the most important in the analysis are *Corbula gibba* and *Ostrea* (Tab. 5). In fact, *Ostrea* has very high fidelity; moreover, in its microenvironment it is the dominant macrobenthic animal. Among the most important taxa there are also: *Pteromeris scalaris,* the lithothamnia, turritellids, corals, and *Turboella.* On the other hand, a great majority of taxa exert only a slight influence on the analysis, which results from either their rarity, evenness of their spatial distribution, or both.

In general, all high-fidelity taxa are well represented by the analysis (Tab. 5). As the matter of fact, these taxa either strongly influence the analysis or are significantly correlated with the taxa important in the analysis. However, many low-fidelity or unimportant in the analysis taxa are underrepresented by the factor-analytic solution, which indicates that the first seven factor axes cannot account for their distribution patterns.

Table 5

Reliability of the R-mode factor analysis of distribution of the Korytnica dominant taxa

Taxon	Actual influence on the analysis	Weight	Quality of representation by the analysis
Corbula	103	346	991
Ostrea	103	6	996
Pteromeris	93	10	995
turritellids	87	72	988
lithothamnia	80	15	970
corals	70	19	989
Turboella	67	61	966
spatangoids	34	44	802
Loripes	32	27	902
cerithiids	29	27	882
Pyrgulina	23	14	644
Lutetia	21	15	402
Dentalium fossile	21	6	119
Odostomia	18	31	710
Ditrupa	18	22	352
Fustiaria	17	33	642
Nassa	14	50	433
Turbonilla	11	25	470
nuculoids	11	6	828
Caecum	11	6	762
Sandbergeria	11	5	730
Circulus	11	5	382
Limopsis	11	1	988
Alvania	10	27	459
bryozoans	9	14	342
Venus	8	17	472
Cingula	8	8	476
naticids	7	38	590
Anadara	7	19	298
Ringicula	7	7	335
cardiids	7	6	323
Dentalium sp.div.	7	1	953
Anomia	6	3	236
Raphitoma	5	12	457
Montacuta	5	2	244
vermetids	5	1	931
Clavatula	4	2	693
Phacoides	4	1	804
Eulima	3	5	608
muricids	1	1	125

When the set of dominant Korytnica taxa is considered in the abstract space of first seven factors, a few distinct groups of taxa can be easily recognized. Each of these groups is to be regarded as representing a faunal association typical of a single assemblage or subassemblage. However, there remains a group of low-fidelity taxa which are usually unimportant in and underrepresented by the analysis; these taxa cannot be regarded as indicative of any assemblage. The faunal associations distinguished by this analysis appear well correlated with the empirical distribution patterns of individual taxa (*cf.* Fig. 4), which supports the reliability of the factor analysis.

When autecology of the analysed taxa taken into account, the environmental gradients underlying the factor axes can be identified. In fact, each abstract factor axis can be thought of as an environmental factor or ecospace dimension limiting the abundance of one faunal association while favorable or at least harmless with respect to another one.

The first factor axis (Fig. 8) is strongly correlated with the abundance of animals inadapted to live in turbid water. It is negatively correlated with the abundance of Corbula gibba which is unusually tolerant of high turbidity. Hence, this axis is to be regarded as reflecting mainly the gradient in water turbidity. However, high positive loadings on this axis are generally possessed by either sessile animals (the corals, oysters, vermetids) or taxa of weak burrowing ability and low escape potential (*Limopsis anomala, Pteromeris scalaris).* On the other hand, the analysis of mortality pattern of *Corbula gibba* demonstrates that this population was periodically affected by an environmental factor which might represent an increase in local sedimentation rate (Hoffman 1976b). Therefore, the first factor axis may also reflect a gradient in local sedimentation rate. The apparent correlation between water turbidity and local sedimentation rate suggests that the former parameter was not dependent upon water turbulence and bottom-deposit resuspension. Presumably it was rather dependent upon mud influx to the basin, that is upon some hydrographic or climatic conditions. The high positive loadings of *Dentalium* sp. div. (mainly *Dentalium badense*) on the first factor axis contrast with the negative loadings of the other scaphopod taxa. This may indicate that these scaphopod groups differed in either burrowing ability or resistance to water turbidity. These scaphopod groups could also differ in their preferred food resources, the microbenthos being distributed accordingly to water turbidity or substrate type. The relatively high positive loading of *Clavatula* indicates probably that these carnivorous gastropods fed mainly on some benthic animals limited by water turbidity, substrate type, or sedimentation rate.

The second factor axis (Fig. 8) is strongly correlated with the abundance of diversified browsing gastropods, which indicates that it is to be regarded as reflecting mainly the abundance of marine plants. Body fossils of marine angiosperms have never been found in the Korytnica Clays. Nevertheless, the root etchings observed commonly on the mollusk shells indicate clearly (*cf.* Cottrell 1977) that benthic plants were represented not only by different algae but also by the seagrasses. Thus, high negative loading of a taxon on the second factor axis demonstrates that environment inhabited by the seagrasses was unsuitable for the settlement by a large population of this taxon. As the matter

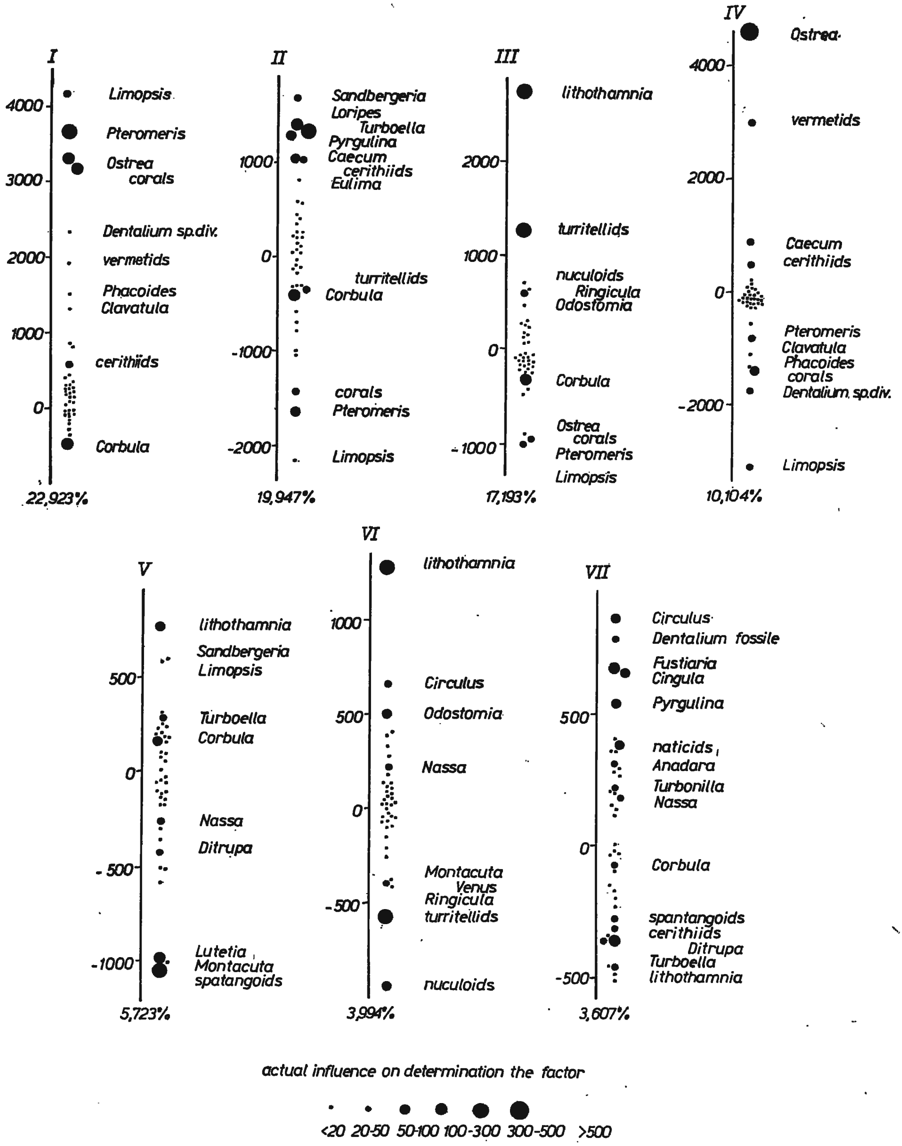


Fig. 8. R-mode factor analysis of distribution of the Korytnica dominant taxa: relationships between the factor axes and taxa

of fact, *Limopsis anomala* appears to prefer deep-water habitats. A dense cover of the seagrasses results in a significant decrease in water circulation. Therefore, it makes the environment inaccessible for such inefficient suspension feeders as *Corbula gibba* or the oysters. Because of the same reason, corals could not flourish among the Korytnica seagrasses. On the other hand, *Loripes dentatus niveus* fed probably very efficiently upon suspended particulate organic matter, which allowed it to outcompete *Corbula gibba.* Its prepotency might also result from some other physical-chemical factors (low oxygen capacity, high pH, etc.) related to the presence of seagrasses (*cf.* Allen 1958; Jackson 1970, 1972; Bretsky 1976). The high positive loadings of parasitic gastropods *Pyrgulina interstincta* and *Eulima subulata* indicate that their unpreserved soft-bodied hosts (polychaetes and holothurians, respectively) were adapted to live among the seagrasses.

The third factor axis (Fig. 8) is strongly correlated with the abundance of fragmented lithothamnian colonies reflecting proximity of very high-energy environments. It is also strongly correlated with the abundance of turritellids and highly mobile infaunal animals. On the other hand, it is inversely related to the abundance of more or less sessile, quiet-water benthos which is unable to resist even a small depth of sudden burial, that is to withstand the stress of a changing configuration of sediment-water interface. Hence, the third factor axis may be postulated to reflect mainly just the temporal variability of bottom microrelief, which could result from either a gradient in substrate firmness, differential environmental energies, or both. This factor axis may also be related to a gradient in bathymetry. As the matter of fact, it allows a sharp distinction between relatively deep-water taxa (such as *Limopsis anomala* or the flabellid corals) and mostly nearshore taxa (such as the lithothamnia or turritellids). On the other hand, very low loadings of most suspension feeders may be related to their exclusion by dense populations of turritellids, due to an intense competition for available space. The high positive loading of parasitic gastropod *Odostomia* indicates that its unpreserved soft-bodied hosts (polychaetes) were adapted to live with dense turritellid populations. A similar explanation may account for the high positive loading of carnivorous gastropod *Ringicula auriculata buccinea.*

The fourth factor axis (Fig. 8) makes a sharp distinction between the cemented epifaunal taxa and the muddy-bottom taxa of low (if any) escape potential. Hence, this factor axis is to be regarded as reflecting a gradient in water turbulence. The relatively high positive loadings of *Caecum,* the cerithiids, and *Alvania* indicate that some marine plants must have been present in the neighborhood of the environment inhabited by the oysters. All the other Korytnica browsers have negative loadings on this factor axis, which demonstrates that this trophic group displayed a plant specificity buffering the intragroup competition.

The fifth factor axis (Fig. 8) is inversely related to the abundance of in-sediment deposit feeders and scavengers. It is directly related to the abundance of fragmented lithothamnian colonies reflecting proximity of well-oxygenated high-energy environments. Hence, the fifth factor axis can be regarded as reflecting a gradient in oxygen capacity of nearbottom water layers. In fact, under conditions of land proximity and high terrigenous influx to the basin, abundance of organic matter in bottom deposits depends mainly upon the rate of oxygenation process (*cf.* Seibold & *al.* 1973). The high negative loading of *Montacuta* indicates its association with the spatangoids thus, demonstrating that this bivalve genus has little changed its mode of life since Miocene time. The high negative loading of *Lutetia nitida* and very great influence exerted by it on the determination of this factor, indicate that this extinct bivalve was very tolerant of stagnant waters. Presumably under conditions of higher oxygen capacity it was easily outcompeted by other suspension feeders, which may account for its lower abundance in the other microenvironments of the Korytnica basin. The subspecies *Loripes dentatus niveus* might also be expected to correlate strongly with a factor reflecting low oxygen capacity; while its loading is very low. This may have resulted from its deep-burrowing habit since it is well known that dense populations of spatangoids usually exclude from the environment most other deep burrowers.

Both the sixth and seventh factor axes (Fig. 8) are hardly interpretable in environmental terms.

Thus, the spatial distribution patterns of forty dominant Korytnica taxa appear to have been controlled by several environmental factors. Nevertheless, it will be shown below that highly complex ecological organization involving purely biotic interrelationships exerted also a significant control over structural characteristics of the Korytnica communities.

ECOLOGICAL STRUCTURE OF FOSSIL ASSEMBLAGES

TURBOELLA-LORIPES ASSEMBLAGE

The analysis of this assemblage is based on 9 independent samples (*cf.* Fig. 1 and Tab. 3), most of which were taken in the central part of the basin. Totally, the samples contain more than 4,000 identifiable macrobenthic specimens. Hence, if the simplifying assumptions of random spatial distribution and equal size of all individuals could be accepted, the probability of failure to detect a species representing numerically only 0.1% of the assemblage would be about 3% (Dennison & Hay 1967). In addition, one large sample was also studied quantitatively.

The *Turboella-Loripes* assemblage is to be recognized (*cf.* Fig. 4) by occurrence of three high-fidelity taxa (*Sandbergeria, Turboella,* and *Loripes dentatus niveus*) and some others typically associated with them and attaining their maximum abundance herein (*Pyrgulina interstincta, Anomia ephippium, Cingula,* and *Eulima subulata*). The homogeneity and distinctness are fairly high although the assemblage is rather similar to the *Corbula* and *Corbula*-spatangoid assemblages (*cf.* Fig. 5). However, two distinct subassemblages can be easily distinguished on the basis of relative abundance of *Pyrgulina interstincta* and the scaphopods.

As indicated by the factor analysis (Tabs 1 and 4), the environment inhabited by the *Turboella-Loripes* assemblage was very rich in marine plants. The water was fairly clear and the bottom microrelief was rather stable. The abundant seagrasses should have strongly influenced the environment by lowering oxygen capacity in the nearbottom layers (*cf.* Lynts 1966; Taylor & Lewis 1970; Taylor 1971; Brasier 1975; Parker 1975). On the other hand, the primary production of seagrass communities is usually extremely high due to the abundance of associated algae. In fact, these epiphytic and/or benthic algae make up the main food resource for benthic animals; the bacteria and accumulated detritus also contribute to the main food resource (Lipps & Valentine 1970; Scoffin 1970; Taylor & Lewis 1970; Brasier 1975). The bottom deposit was very homogeneous among the samples, and represented a mud consisting of clay and silt in almost equal proportions (*cf.* Fig. 6); its accumulation was partly due to the trapping activity of seagrasses (*cf.* Ginsburg & Lowenstam 1958; Davies 1970; Scoffin 1970; Warme 1971; Basan 1973). The density of fossil organisms is very high in the samples from within the *Turboella-Loripes* assemblage. However, it was not studied quantitatively because when reliable estimates of the rate of sedimentation are unavailable, one cannot biologically interpret differences in fossil abundance from place to place.

In time-averaged fossil assemblages any precise reconstruction of the abundance hierarchy of an original community is obviously impossible because of differential life spans, mortality patterns, preservabilities etc. Nevertheless, the abundance hierarchy of *Turboella-Loripes* assemblage clearly indicates that at least in the mollusk portion of the original community the individuals were more or less evenly distributed among several taxa (Fig. 9). In fact, in addition to the dominant Korytnica taxa, some other mollusks are also relatively abundant in the samples from within this assemblage. Thus, the bivalves *Meretrix, Glycymeris, Arca,* solenaceans, and pectinids, and the gastropods *Scala, Cerithiopsis, Columbella, Ancilla, Fusus, Ficus, Tornatina,* and *Calyptraea* were found in most samples, although always in minor proportions. In addition to mollusks, the foraminifers are very abundant. As it was shown by Walkiewicz (1975, Fig. 4), the foraminiferal assemblage of the area inhabited by the *Turboella-Loripes* assemblage is dominated by the textulariids, elphidiids, miliolids, and cibicidids; however, the polymorphinids, amphisteginids, and soritids are also present. The abundance of polychaete-attacking pyramidellids indicates that the polychaetes were also common; the presence of holothurians and sponges can also be inferred. In most samples spatangoid fragments, crab claws, and fish otoliths occur. Such a taxonomic composition of the *Turboella-Loripes* assemblage strongly supports the view that this was a seagrass community (Brasier 1975, pers. communication).

Taxonomic diversity of a community is commonly assumed to be among the most important characteristics of community structure. It is assumed to reflect the modal niche width and hence the level of species interactions. As such, it has been thought of as related to environmental predictability or such community characteristics as successional stage or ecological stability (*cf.* Margalef 1968; Sanders 1968, 1969; Slobodkin & Sanders 1969; Bretsky & Lorenz 1970; Johnson 1970). However, thus far little experimental work has been done to prove the necessary relationship between diversity and degree of species interactions (but *see* O'Connor & *al.* 1975). In the present study the mollusk diversity was determined for each fossil assemblage because even although the crucial importance of taxonomic diversity in ecological studies is not proved (*cf.* Jumars 1974; Goodman 1975; Moldenke 1975), it should be extensively studied. In the case of Korytnica mollusks, this approach may be justified despite the taphonomic bias because all the taxa appear to be equally preservable; they represent a very large and ecologically complex portion of the ecosystem, being sensitive of many independent environmental parameters. One should, however, keep in mind that diversity of the Korytnica mollusks cannot be directly compared to the present-day mollusk assemblages.

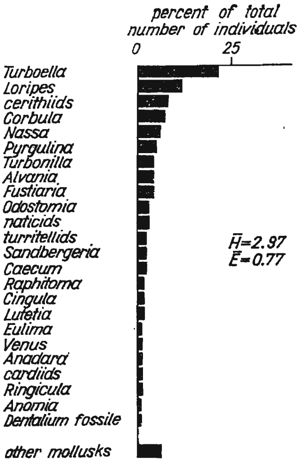
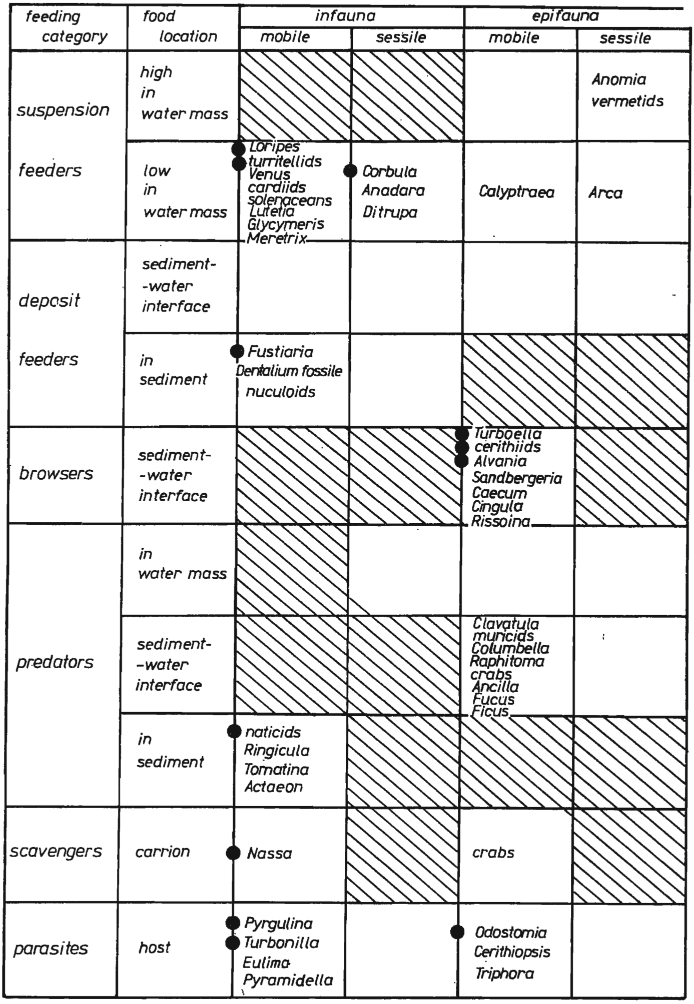


Fig. 9
Average taxonomic composition of the *Turboella-Loripes* assemblage

Shannon's measure of average uncertainty (H) was used to express taxonomic diversity. The evenness (E) of individuals distribution among species was also computed. It was measured by the ratio of Shannon's diversity to logarithm of the number of species; in fact, this ratio does not involve any assumption about the distribution (*cf.* Beerbower & Jordan 1969) as does the coefficient of equitability proposed by Lloyd & Ghelardi (1964).

Both the mollusk diversity and evenness are very high in *Turboella-Loripes* assemblage (Fig. 9). As the matter of fact, these coefficients are near their maximum values reached in the Korytnica assemblages. Totally, about 130 macrobenthic species are present in the samples.

The biovolume dominance of *Turboella-Loripes* assemblage is very low. It seems to be so low as to make inapplicable the very concept of trophic nucleus (*cf.* Neyman 1967). As judged from the biovolume relations, the biomass was originally distributed more or less evenly among the taxa. A dozen of taxa are regarded as dominant herein. However, many other macrobenthic taxa have the biovolume of a similar order.



feeding category	food location	infauna		epifauna	
		mobile	sessile	mobile	sessile
suspension feeders	high in water mass	▨	▨		*Anomia* vermetids
	low in water mass	● *Loripes* ● turritellids *Venus* cardiids solenaceans *Lutetia* *Glycymeris* *Meretrix*	● *Corbula* *Anadara* *Ditrupa*	*Calyptraea*	*Arca*
deposit feeders	sediment--water interface				
	in sediment	● *Fustiaria* *Dentalium fossile* nuculoids		▨	▨
browsers	sediment--water interface	▨	▨	● *Turboella* ● cerithiids ● *Alvania* *Sandbergeria* *Caecum* *Cingula* *Rissoina*	▨
predators	in water mass	▨			
	sediment--water interface	▨	▨	*Clavatula* muricids *Columbella* *Raphitoma* crabs *Ancilla* *Fucus* *Ficus*	
	in sediment	● naticids *Ringicula* *Tornatina* *Actaeon*	▨	▨	▨
scavengers	carrion	● *Nassa*	▨	crabs	▨
parasites	host	● *Pyrgulina* ● *Turbonilla* *Eulima* *Pyramidella*		● *Odostomia* *Cerithiopsis* *Triphora*	

Fig. 10. Trophic-substrate-mobility niches of the *Turboella-Loripes* assemblage
Cross-hatched blocks indicate niches not normally occupied by marine benthic animals; taxa marked by black circles indicate members of the trophic nucleus

The assemblage includes a very wide variety of general adaptive types. Most gross ecological niches available to macrobenthic animals are at least partly occupied (Fig. 10). The dominant macrobenthic taxa are more or less evenly distributed among different adaptive and trophic groups. Thus, in terms of ecological classifications of benthic communities, the *Turboella-Loripes* assemblage is extremely heterogeneous. In fact, many trophic groups played significant roles in the trophic structure (Fig. 11). This is, indeed, supported by the low value of index of trophic uniformity, that is dispersion of the total biomass (or biovolume) among trophic groups (Nesis 1965). The value of this index is in part a function of the number of possible trophic groups defined by the worker; in this study ten trophic categories were used. Then, the index (σ^2) is 225 for the *Turboella-Loripes* asemblage. It was probably even lower in the original community since unpreserved sponges, polychaetes, and holothurians contributed to the suspension-feeding and deposit-feeding groups.

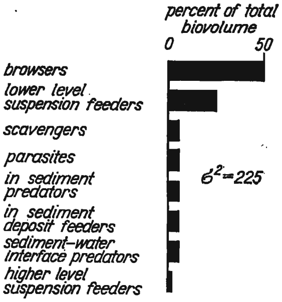


Fig. 11
Dispersion of the biovolume among trophic categories in the *Turboella-Loripes* assemblage

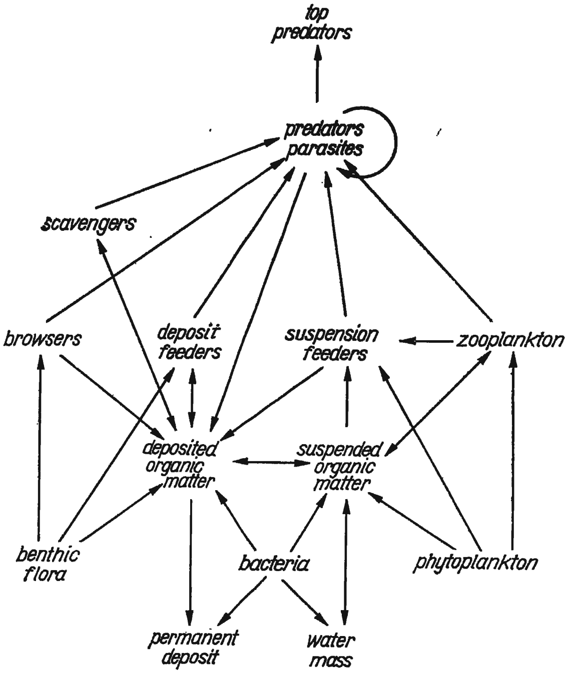


Fig. 12
Simplified model of nutrient cycle in a shallow-water benthic ecosystem

A simplified model of nutrient cycle in a marine shallow-water benthic ecosystem (Fig. 12) shows clearly the main trophic subwebs (*sensu* Paine 1966). However, in such ecosystems even low-level predators feed often on animals from different subwebs thus, causing an interdependence among these portions of the structure. From this model one can also deduce the nature of relationships between the structure of a benthic community and environmental characteristics of its biotope (*cf.* Hoffman & Szubzda 1976).

When unpreserved portions of the ecosystem taken into account, the three main subwebs can be easily recognized in the trophic structure of *Turboella-Loripes* community (Fig. 13). In fact, they appear to have played equally important roles in energy flow through the ecosystem. Many suspension-feeding populations, mainly polychaetes were violently attacked by the parasites which formed eventually an additional member of the suspension-feeding subweb. On the other hand, the deposit-feeding subweb can be further subdivided into scavenger food-chain and deposited-detritus feeder food-chain. To an extent, the latter one intergrades also with the browsing subweb. The browsing and deposit-feeding subwebs have their own keystone predators, namely the pleurotomids and naticids, respectively. The suspension-feeding subweb can, however, be subdivided into two food-chains dependent upon either the pleurotomids (epifaunal food-chain) or the naticids (infaunal food-chain). All these subwebs share the same top predator, that is the pagurid crabs.

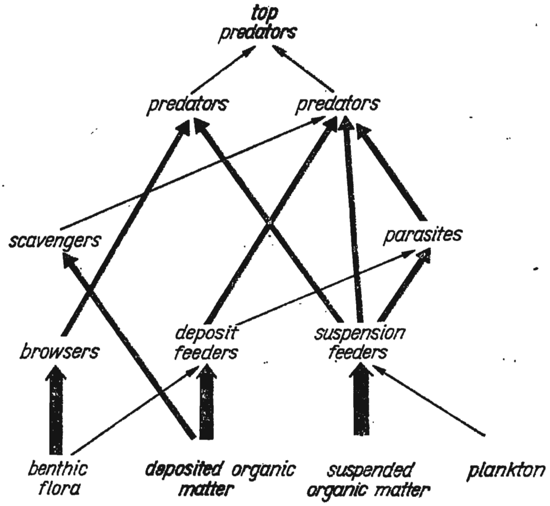


Fig. 13
Simplified trophic web of the *Turboella-Loripes* assemblage; width of the arrows indicates relative significance of the paths

A more detailed reconstruction of the trophic structure (Fig. 14) demonstrates that actually the structure was much more complex. However, this reconstruction is also somewhat simplified since only the adults and only the main feeding habits of each taxon are considered. Furthermore, the microbenthos is omitted while it does generally also exhibit an extremely complex trophic structure (*cf.* Mare 1942; Fenchel 1969). In general, the competition for food was significantly buffered, and food resources available were entirely exploited in the *Turboella-Loripes* ecosystem. Thus, the pleurotomid and muricid gastropods fed mainly upon the browsers and semi-infaunal or shallow-burrowing suspension feeders. The naticids fed mainly upon the semi-infaunal or infaunal suspension feeders and infaunal parasitic pyramidellids. The actaeonacean gastropods fed mainly upon epifaunal pyramidellids, benthic foraminifers, and polychaetes. Hence, the feeding competition among different groups of predators was restricted to narrow transitional ecozones, which allowed the co-existence of their large populations. The polychaetes and sponges made up the main food resource for parasitic gastropods. Among the browsers the competition for food could be buffered by their plant specificity (*cf.* Duffus 1969). Among the deposited-detritus feeders the competition was buffered due to the depth stratification of their feeding niches. In fact, the spatangoids and holothurians burrow deeply in

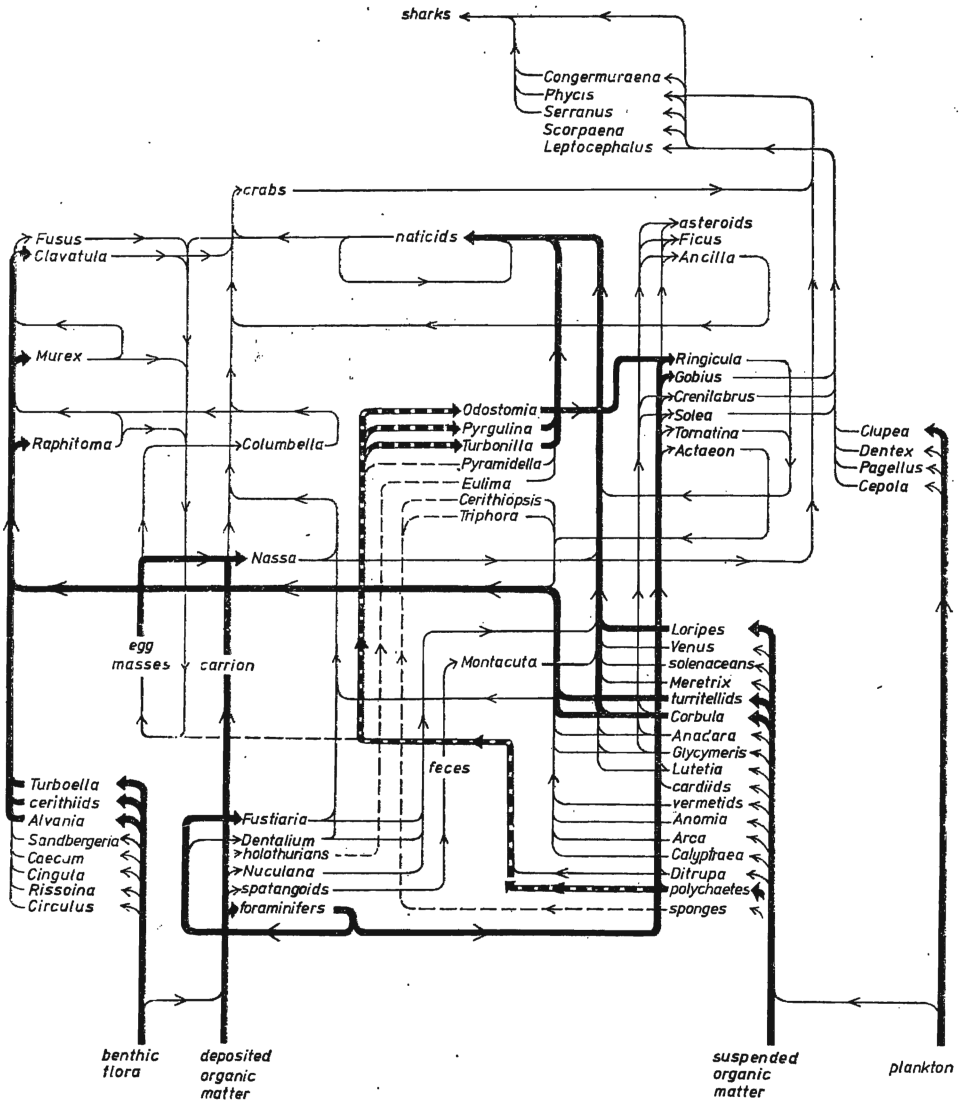


Fig. 14. More complete trophic web of the *Turboella-Loripes* assemblage; width of the arrows indicates relative significance of the paths; broken lines indicate inferred members of the community

the sediment in search of food particles; the scaphopods and small nuculanids feed at a depth of a few centimeters below the sediment-water interface; the benthic foraminifers live at or very near the sediment-water interface. The suspension-feeding niche made an exception since it was only insignificantly subdivided. All the dominant suspension feeders fed probably at the same level, namely just above the sediment-water interface, and upon the same food resources. Such a situation appears to occur commonly in suspension-feeding portions of benthic ecosystems, which prompted Levinton (1972, 1974) and Stanley (1973) to postulate that suspension-feeding animals should not participate at all in competitive interactions for food. However, among suspension feeders a competition for food can also be released due to superabundance of food resources (Nesis 1965; Neyman 1967; Walker 1972), which may, indeed, be expected under conditions of land proximity and seagrass cover. Benthos makes obviously part of an ecosystem including the overlying water mass. Therefore, the trophic position of Korytnica fish is also considered in the reconstruction. Some fish formed an independent plankton-feeding subweb; others were the predators in the suspension-feeding subweb. Both these groups were eaten by the carnivorous fish among which the small sharks occupied the highest trophic position.

Fig. 15. Spatial relations among the infauna in the *Turboella-Loripes* assemblage

Competition for available space is usually most intense in hard-bottom communities. However, it was recently demonstrated that on soft bottoms a competition for space may also significantly influence the structure of benthic communities (Levinton & Bambach 1975; Stump 1975). In the *Turboella-Loripes* community the space-related competition was probably somewhat buffered since the dominant infaunal animals lived at different depths below the sediment-water interface (Fig. 15); whereas the epifaunal animals were mostly mobile and lived either at the sediment-water interface and amongst the rhizomes and stem bases of the seagrasses (*Caecum, Sandbergeria,* the muricids, pleurotomids, *Odostomia* etc.), or at the seagrass blades (the rissoids, cerithiids etc.).

Thus, under the conditions of very high supply of unusually diversified food resources, and significant variability of physical-chemical environment, highly complex and integrated ecological structure developed. Presumably it was also fairly stable (in the sense of short-term persistence stability of Margalef 1969). Nevertheless, among the mollusk populations of *Turboella-Loripes* community there were both *K*-selected and *r*-selected populations (*cf.* Hoffman 1976b, c).

The taxonomic composition and ecological structure of *Turboella-Loripes* community resemble very closely the present-day macrobenthic communities of tropical or subtropical seagrass beds (*Thalassia* or *Cymodocea* associations of Brasier 1975). As the matter of fact, these communities are usually extremely complex in their ecological structure. The trophic web consists of several more or less interdependent food-chains. They are strongly dominated in number by small browsing gastropods (mainly the cerithiids, rissoids, and neritids) and small lucinoid bivalves. However, endobyssate bivalves such as the pinnids, and epifaunal suspension feeders are also common. Deposit feeders are usually represented by the tellinid bivalves and soft-bodied polychaetes and holothurians. Predators are extremely diversified and abundant. They are represented mainly by the naticid, actaeonacean, muricid, conid, pleurotomid, and cypraeid gastropods; however, the starfish and predatory crabs are also abundant. The scavenging buccinids are very common. The foraminiferal assemblages consisting of the soritids, miliolids, and cibicidids are very typical of these seagrasses. In most communities the competition for both food and space is minimized owing to subdivisions of the gross ecological niches (*cf.* Macnae & Kalk 1962b; Lewis & Taylor 1966; O'Gower & Wacasey 1967; Taylor 1968, 1971; Taylor & Lewis 1970; Jackson 1972; Brasier 1975).

On the other hand, the temperate-zone seagrass beds (*Zostera* association of Brasier 1975) are characterized by somewhat different macrobenthic communities. In these communities suspension-feeding bivalves occur in minor amounts when compared to the browsing gastropods and epifaunal (mainly epiphytal) suspension feeders (*cf.* Allee 1923; Lewis 1964; Warme 1971; Rasmussen 1973; Parker 1975); the soritids and other large foraminifers are absent (Brasier 1975). Very similar communities are also reported from the kelp beds (Lewis 1964; Hagerman 1966; Vohra 1971).

Benthic assemblages associated with marine angiosperms are known in the fossil record at least since the Eocene time. In fact, already the Upper Cretaceous carbonate banks of Normandy (Kennedy & Juignet 1974) may have originated mainly due to the trapping and stabilizing activity of seagrasses. However, unquestionable body fossils of the marine angiosperms were reported from the Eocene of the Paris Basin (Den Hartog 1970), English Channel (Curry 1965), and Florida (Randazzo & Saroop 1976). The trace fossils were also recorded in the Miocene of Maryland (Cottrell 1977). Several other Tertiary benthic assemblages were postulated to represent seagrass communities, mostly on the basis of their foraminiferal faunas (Bhatia 1957; Wright & Murray 1972; Brasier 1975). However, the ecological structures of associated macrobenthic assemblages have never been described in detail. One may only postulate that the fossil assemblage of the Eocene Calcaire Grossier of the Paris Basin (*cf.* Pomerol 1973) is very alike the discussed assemblage. On the other hand, the Pleistocene estuarine-lagoonal assemblage of the South Africa (Tankard 1975) may represent either a community of *Turboella-Loripes* type, or one intermediate between the *Turboella-Loripes* and *Corbula*-spatangoid types.

CORBULA ASSEMBLAGE

The following analysis is based on 20 independent samples (*cf.* Fig. 1 and Tab. 3), all of which were taken in the central part of the basin. In addition, one large sample was also analysed quantitatively.

The *Corbula* assemblage contains only low-fidelity taxa (Fig. 4). It is to be recognized by very high abundance of *Corbula gibba*, maximum abundances of *Fustiaria miocaenica, Dentalium fossile,* and the naticids, and absence or very low abundance of the spatangoids, *Turboella,* or *Loripes dentatus niveus.* The homogeneity and distinctness are very low and as the whole the *Corbula* assemblage is fairly similar to the *Corbula*-spatangoid and *Turboella-Loripes* assemblages (*cf.* Fig. 5). However, two distinct subassemblages can be easily distinguished on the basis of relative abundance of the scaphopods. The *Corbula* subassemblage is described after 6 samples containing totally about 1,800 identifiable macrobenthic specimens; hence, if the simplifying assumptions could be accepted, the probability of failure to detect a species representing numerically only 0.25% of the assemblage would be about 3% (Dennison & Hay 1967). The *Corbula*-scaphopod subassemblage is described after 14 samples containing totally about 7,000 identifiable macrobenthic specimens; hence, the probability of failure to detect a species representing numerically only 0.1% of the assemblage is about 0.1%. Generally, the density of fossils is very high; it is low only in the samples *7, 10,* and *12* from within the *Corbula* subassemblage.

As indicated by the factor analysis (Tabs 1 and 4), the environment inhabited by the *Corbula* subassemblage was characterized by very turbid water. Marine plants were absent, and the bottom microrelief was rather stable. The bottom sediment was fairly poor in organic matter, which may be due to relatively high redox potential. The analysis of mortality pattern of *Corbula gibba* appears to indicate that the terrigenous influx was periodically increasing probably due to a climatic or hydrographic periodicity (Hoffman 1976b). The biotope of

Corbula-scaphopod subassemblage was somewhat more similar to that of *Turboella-Loripes* assemblage. The substrate was fairly homogeneous among the samples from within the *Corbula* assemblage, and represented mud consisting of silt and clay in almost equal proportions (*cf.* Fig. 6).

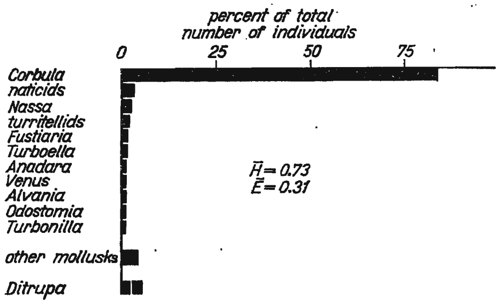


Fig. 16
Average taxonomic composition of the *Corbula* subassemblage

The *Corbula* subassemblage consists mostly of *Corbula gibba* itself; in fact, this species represents more than 80% of the total number of mollusk individuals (Fig. 16). Thus, the numerical dominance is extremely high. It is much lower in the *Corbula*-scaphopod subassemblage (Fig. 17) since *Corbula gibba* represents less than 50% of the subassemblage, while five other mollusk taxa represent jointly about 25% of the total number of individuals. Most dominant Korytnica taxa are present in the samples from within the *Corbula*-scaphopod subassemblage, although always in minor proportions. Moreover, the bivalves *Meretrix, Glycymeris,* and *Anomia,* and the gastropods *Scala, Columbella, Ancilla, Fusus, Tornatina,* and *Actaeon* were found in many samples. In addition to the macrobenthos the foraminifers are also very abundant. In most samples the fish otoliths occur.

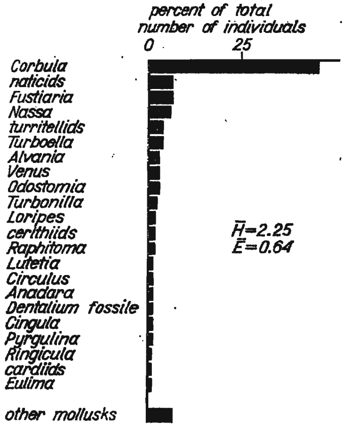


Fig. 17
Average taxonomic composition of the *Corbula*-scaphopod subassemblage

Both the mollusk diversity and evenness of the *Corbula* subassemblage are extremely low (Fig. 16); in fact, the values of these coefficients are the least of the whole Korytnica Clays. They are considerably higher in the *Corbula*-scaphopod subassemblage (Fig. 17). Totally, about 80 macrobenthic species are present in the samples from within the *Corbula* assemblage.

The biovolume dominance hierarchy of *Corbula* assemblage resembles very closely the hierarchy in numerical abundance. Thus, the biovolume dominance is very high. In fact, *Corbula gibba* itself represents predominant portion of the total biovolume and hence, it is to be regarded as the single member of monospecific trophic nucleous.

feeding category	food location	infauna		epifauna	
		mobile	sessile	mobile	sessile
suspension feeders	high in water mass	▨	▨		*Anomia* bryozoans
	low in water mass	turritellids *Venus* *Meretrix* *Loripes* *Lutetia* cardiids	● *Corbula* *Anadara* *Ditrupa*		
deposit feeders	sediment-water interface				
	in sediment	*Fustiaria* *Dentalium fossile* spatangoids		▨	▨
browsers	sediment-water interface	▨	▨	*Turboella* *Alvania* cerithiids *Circulus* *Cingula*	▨
predators	in water mass	▨			
	sediment-water interface	▨	▨	*Raphitoma* *Clavatula* muricids *Columbella* *Ancilla* *Fusus*	
	in sediment	naticids *Ringicula* *Tornatina* *Actaeon*	▨	▨	▨
scavengers	carrion	*Nassa*	▨		▨
parasites	host	*Turbonilla* *Pyrgulina* *Eulima*		*Odostomia*	

Fig. 18. Trophic-substrate-mobility niches of the *Corbula*-scaphopod subassemblage
Cross-hatched blocks indicate niches not normally occupied by marine benthic animals; taxa marked by black circles indicate members of the trophic nucleus

The *Corbula*-scaphopod subassemblage includes a wide variety of general adaptive types. Most gross ecological niches available to macrobenthic animals are partly occupied (Fig. 18). As the matter of fact, despite the predominance of lower level suspension feeders, the Nesis' index of trophic uniformity is very low; its value is only 2.10, that is it is of the same order as in the *Turboella-Loripes* assemblage. This is due to the high dispersion of biovolume among the minor trophic groups (Fig. 19). The *Corbula* subassemblage contains less ecologically variable fauna. The predominance of lower level suspension feeders is much

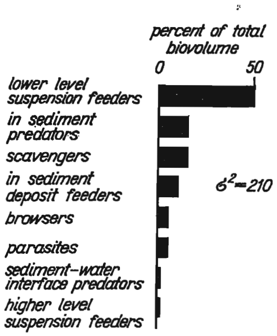


Fig. 19
Dispersion of the biovolume among trophic categories in the *Corbula*-scaphopod subassemblage

feeding category	food location	infauna mobile	infauna sessile	epifauna mobile	epifauna sessile
suspension feeders	high in water mass	▨	▨		
	low in water mass	turritellids Venus	● Corbula Anadara Ditrupa		
deposit feeders	sediment-water interface				
	in sediment	Fustiaria spatangoids		▨	▨
browsers	sediment-water interface	▨	▨	Turboella Alvania cerithiids	▨
predators	in water mass	▨			
	sediment-water interface	▨	▨	Raphitoma	
	in sediment	naticids Ringicula Tornatina	▨	▨	▨
scavengers	carrion	Nassa	▨		▨
parasites	host	Turbonilla		Odostomia	

Fig. 20. Trophic-substrate-mobility niches of the *Corbula* subassemblage
Cross-hatched blocks indicate niches not normally occupied by marine benthic animals; taxa marked by black circles indicate members of the trophic nucleus

more distinct (Figs 20 and 21). Indeed, the index of trophic uniformity is very high; it reaches the value of 640.

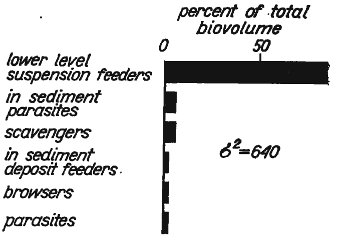


Fig. 21
Dispersion of the biovolume among trophic categories in the *Corbula* subassemblage

Thus, the trophic structure of *Corbula* subcommunity was very simple. Actually, it consisted mainly of the simple and short suspension-feeder food-chain, whereas all other food-chains played only minor roles in the energy flow (Fig. 22). The trophic structure of *Corbula*-scaphopod subcommunity (Fig. 23) was already more complex since it consisted of two distinct subwebs, namely the suspension-feeding and deposit-feeding ones. The suspension-feeding subweb was, however, much more important. The deposit-feeding subweb can be further subdivided into scavenger food-chain and deposited-detritus feeder food-chain, the former one being more important. The browsing subweb was also present but it was of negligible importance in the energy flow. Both the suspension-feeding

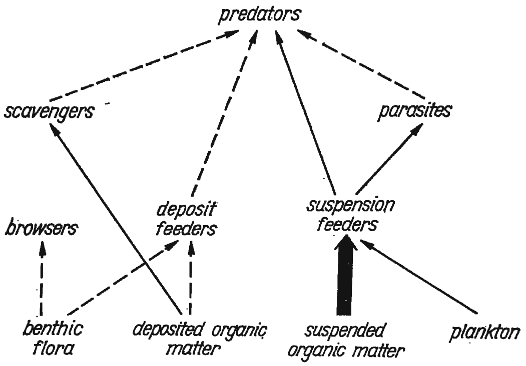


Fig. 22
Simplified trophic web of the *Corbula* subassemblage; width of the arrows indicates relative significance of the paths

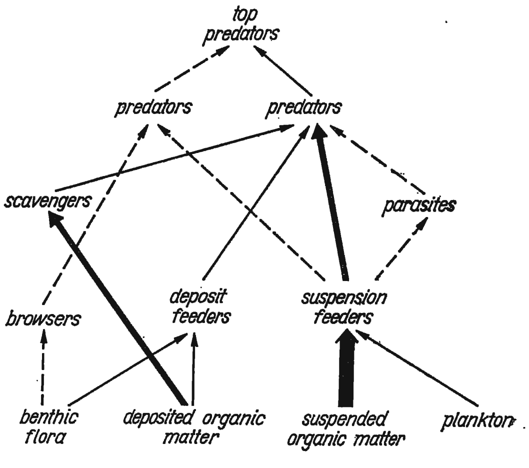


Fig. 23
Simplified trophic web of the *Corbula*-scaphopod subassemblage; width of the arrows indicates relative significance of the paths

and deposit-feeding subwebs shared the same predators, namely the naticids. Some other predators, such as the pleurotomids or muricids, fed mainly on the suspension feeders. This simplified diagram of the trophic structure indicates that in the *Corbula*-scaphopod subcommunity the degree of interspecific competition for food was fairly low. However, this appears to have resulted notasmuch from biotic interactions leading to niche subdivisions, as from the domination of gross ecological niches by single taxa. Moreover, the interdependence of different food-chains was probably much weaker than in the *Turboella-Loripes* community. Hence, despite the similar values of trophic uniformity, the complexities of trophic structure appear to have been very different between the *Turboella-Loripes* and *Corbula*-scaphopod communities.

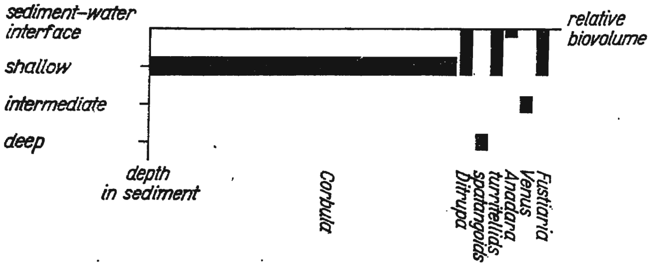


Fig. 24. Spatial relations among the infauna in the *Corbula* subassemblage

Neither in the *Corbula* nor *Corbula*-scaphopod subcommunities the competition for available space was buffered (Figs 24 and 25). In fact, most infaunal animals lived at approximately the same depth below the sediment-water interface. The dense populations of *Corbula gibba* must have restricted the feasibility of settlement the substrate by other infaunal or semi-infaunal animals. This competitive situation for space could also indirectly influence the trophic structure by making the biotope more or less inaccessible for most deposit feeders.

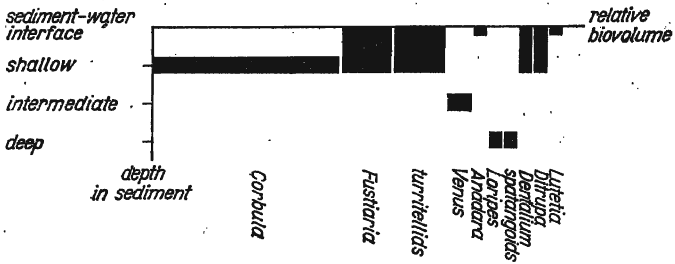


Fig. 25. Spatial relations among the infauna in the *Corbula*-scaphopod subassemblage

Benthic assemblages similar in taxonomic composition and ecological structure to the *Corbula* assemblage are known in the fossil record at least since the Early Cretaceous time. Scott (1970, 1974) described from the Lower Cretaceous mudstones of the southern United States recurrent fossil assemblages dominated by the corbulid and breviarcid bivalves. The numerical dominance (and probably the biovolume dominance, too) is very high. In addition to these two dominant bivalve groups, the assemblages contain also the cardiid bivalves and turritellid gastropods occurring in minor proportions. Thus, these assemblages appear to have possessed very simple trophic structures consisting exclusively of short suspension-feeder food-chains. The species diversity is fairly low. The density of fossils is high. All these assemblages were interpreted by Scott (1970, 1974) as representing nearshore, lower shoreface communities.

Very similar assemblages were also reported by Hecker & *al.* (1962, 1963) from the Lower Paleogene shallow sublittoral clays of the Fergana Basin, Soviet Union. In fact, the *Corbula karaunkurica* association is strongly dominated by the index species. In addition, it contains also some naticid gastropods and carditid bivalves; sometimes the browsing gastropods *Potamides* occur in minor amounts. Thus, the taxonomic diversity is very low. The trophic structure was very simple and consisted mainly of the suspension-feeder food--chains dependent upon the naticids as the keystone predators.

Benthic assemblages resembling strikingly the *Corbula* subassemblage of the Korytnica Clays were also described by Boekschoten (1963) and Báldi (1973) from the Oligocene shallow sublittoral clays of the Netherlands and Hungary, respectively.

Both Scott (1970, 1974) and Báldi (1973) paralleled the extinct assemblages dominated by the corbulids with the present-day *Syndosmya* Community of Thorson (1957). In fact, both community types are typical of sheltered or estuarine areas where they occur on muddy bottoms of the shallow sublittoral zone; they are also both characterized by the domination by distinctly opportunistic species enormously fluctuating in population size (*cf.* Ford 1923; Stephen 1933, 1934; Jones 1952). Nevertheless, it seems that the very natures of these two community types are quite different. The corbulid assemblages fed mainly upon seston and were strongly dominated by fairly sessile animals; any mechanisms buffering competition for food or space were lacking in their structures. In contrast, the dominant members of the extant *Syndosmya* Community feed mainly upon bacteria and deposited detritus (*Syndosmya, Nucula, Echinocardium*). Moreover, the deposit-feeding niche appears to be distinctly subdivided with respect to food location since *Syndosmya* feeds at the sediment-water interface; whereas *Nucula* feeds shallowly; and *Echinocardium* feeds deeply in the sediment. Thus, the trophic structure of a typical *Syndosmya* Community seems significantly more complex and integrated than that of the corbulid assemblages. On the other hand, *Syndosmya* Communities contain usually many vagile animals, and competition for available space seems to be rather buffered due to spatial stratification of living positions of the dominant community members.

CORBULA-SPATANGOID ASSEMBLAGE

The following analysis of this assemblage is based on 6 independent samples (*cf.* Fig. 1 and Tab. 3) which contain almost 2,400 identifiable macrobenthic specimens (however, the abundance of spatangoids cannot be determined quantitatively). Therefore, the probability of failure to detect a species representing numerically only 0.25% of the assemblage is about 2% (Dennison & Hay 1967).

The *Corbula*-spatangoid assemblage is to be recognized (*cf.* Fig. 4) by very high abundances of fairly high-fidelity taxa such as *Lutetia nitida,* the spatangoids, *Ditrupa cornea,* or *Montacuta.* In addition, some low-fidelity taxa are typically associated with this assemblage and attain their maximum abundances herein (*Nassa, Venus multilamella marginalis, Anomia ephippium,* the cardiids). Abundances of *Corbula gibba, Anadara diluvii, Turbonilla,* and *Odostomia* are also near their maximum values. The distinctness is fairly low, and the assemblage is, indeed, very similar to the *Corbula* assemblage (*cf.* Fig. 5). However, the homogeneity is rather high. The density of fossils is also fairly high.

As indicated by the factor analysis (Tabs 1 and 4), the bottom sediment settled by the *Corbula*-spatangoid assemblage was very rich in organic matter. The water was fairly turbid, seagrasses were absent, and water turbulence was negligible. All this suggests that the redox potential at the sediment-water interface was low. Nevertheless, the presence of some browsing gastropods indicates that despite the reducing conditions beneath the sediment-water interface, some algae were able to cover the sediment surface; such an inference is also supported by the abundance of suspension-feeding animals which are normally unable to resist the stress of poorly oxygenated waters. In fact, this is a fairly common situation of soft bottoms of very sheltered sites (*cf.* Taylor

1971). The substrate was very homogeneous among the samples and represented silty clay (Fig. 6).

The assemblage is strongly dominated by *Corbula gibba* which represents 40% of the total number of mollusk individuals, and the spatangoid echinoids (Fig. 26). Thus, the numerical dominance is high. In addition to the dominant taxa, the cassidid and actaeonacean gastropods were found in the samples. The foraminifers are also very abundant. The abundance of actaeonacean and pyramidellid gastropods may suggest that soft-bodied polychaetes they usually feed upon were also common. In most samples the fish otoliths occur.

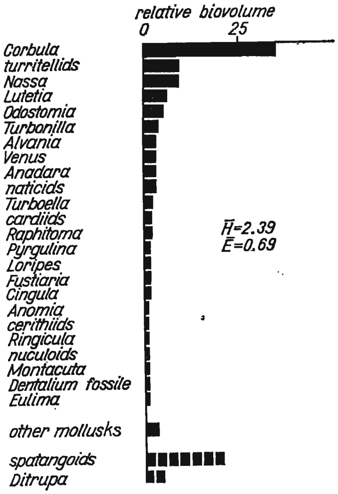


Fig. 26
Average taxonomic composition of the *Corbula*-spatangoid assemblage

Despite the high abundance of *Corbula gibba* itself, the mollusk diversity is high (Fig. 26). Totally, about 70 macrobenthic species are present in the samples from within the *Corbula*-spatangoid assemblage.

The biovolume dominance seems fairly high. The spatangoids, *Corbula gibba*, the turritellids, and *Nassa* are thought to form the trophic nucleus. The next dominant positions in the biovolume dominance hierarchy are occupied by *Ditrupa cornea*, *Odostomia*, *Turbonilla*, the naticids, and *Venus multilamella marginalis*.

The *Corbula*-spatangoid assemblage consists mainly of infaunal animals (Fig. 27). Nevertheless, the trophic nucleus is distinctly heterogeneous. It consists of suspension feeders, in-sediment deposit feeders, and scavengers. Moreover, the parasites and in-sediment predators played also fairly significant roles in the trophic structure (Fig. 28). Hence, the index of trophic uniformity is low; its value is only 200. However, the trophic structure (Fig. 29) was significantly less complex and integrated than that of *Turboella-Loripes* community. It consisted mainly of the suspension-feeding and deposit-feeding subwebs. The pyramidellid parasites formed eventually an additional member of the suspension-feeding subweb. The suspension-feeding subweb was primarily dependent upon the predation by naticids and *Ringicula auriculata buccinea*. In fact, among the top predators of suspension-feeding subweb a dietary specialization appears to have existed since the naticids attacked almost exclusively the infaunal mollusks, whereas *Ringicula auriculata buccinea* fed probably upon the soft-bodied polychaetes, foraminifers, and *Odostomia*. The deposit-feeding subweb can be further subdivided into scavenger food-chain and deposited-detritus feeder food-chain, the latter one being much more important in the structure. Moreover, the

feeding category	food location	infauna		epifauna	
		mobile	sessile	mobile	sessile
suspension feeders	high in water mass	▨	▨		Anomia
	low in water mass	● turritellids Venus Lutetia Montacuta cardiids	● Corbula Anadara Ditrupa		
deposit feeders	sediment-water interface				
	in sediment	● spatangoids Fustiaria nuculoids Dentalium fossile		▨	▨
browsers	sediment-water interface	▨	▨	Alvania Turboella Cingula	▨
predators	in water mass	▨			
	sediment-water interface	▨	▨	Raphitoma Clavatula	
	in sediment	naticids Ringicula Tornatina Semicassis	▨	▨	▨
scavengers	carrion	● Nassa	▨	crabs	▨
parasites	host	Turbonilla Eulima Eulimella		Odostomia	

Fig. 27. Trophic-substrate-mobility niches of the *Corbula*-spatangoid assemblage
Cross-hatched blocks indicate niches not normally occupied by marine benthic animals; taxa marked by black circles indicate members of the trophic nucleus

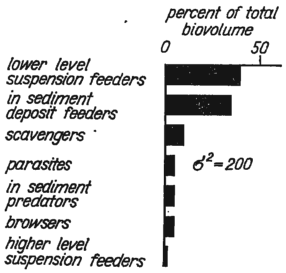


Fig. 28
Dispersion of the biovolume among trophic categories in the *Corbula*-spatangoid assemblage

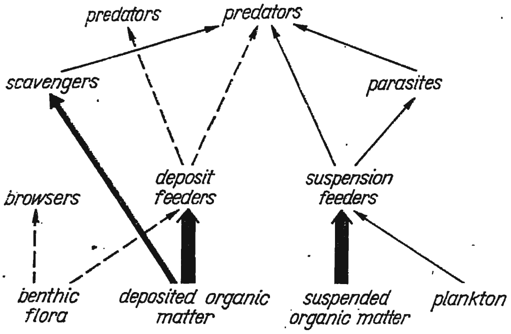


Fig. 29
Simplified trophic web of the *Corbula*-spatangoid assemblage; width of the arrows indicates relative significance of the paths

in-sediment deposit-feeding niche was subdivided with respect to food location since the scaphopods fed probably not as deeply in the sediment as did the spatangoids. This feeding niche was also subdivided with respect to food resources utilized since the scaphopods fed mainly upon living or dead microbenthos, while the spatangoids fed mainly on detrital organic particles and bacteria. The scavenger food-chain shared the keystone predator (namely, the naticids) with the suspension-feeding subweb. However, the deposited-detritus feeding spatangoids were dependent upon their own predators, the cassidid gastropods. The browsing subweb was unimportant.

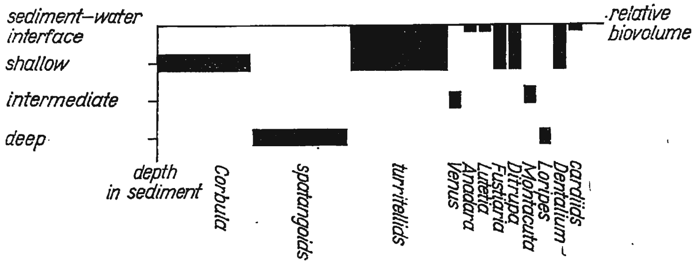


Fig. 30. Spatial relations among the infauna in the *Corbula*-spatangoid assemblage

The competition for space below the sediment-water interface appears to have been somewhat buffered because the dominant infaunal animals lived at different depths in the sediment (Fig. 30).

In general, despite the relatively low degree of biotic co-adaptation among the consumers of a single trophic level, the competition for resources was very low if any. This was probably due to the highly restrictive physical-chemical environment which allowed only some taxa to flourish. In its turn, this resulted in the domination of most gross ecological niches by single taxa, and led to the low degree of interdependence among community members. Only in-sediment deposit feeders were somewhat interdependent. Nevertheless, among the constituent populations there were both *r*-strategists and *K*-strategists (*cf.* Hoffman 1976b, c).

The *Corbula*-spatangoid assemblage can be paralleled with the *Syndosmya* Community of Thorson (1957) but more specifically with its variety transitional to the *Amphiura* Community (*cf.* Ford 1923). In fact, present-day communities of this type inhabit usually silty clayey bottoms, often in waters characterized by low oxygen capacity and bad circulation. Their trophic structures consist mainly of distinct and equally important deposit-feeding and suspension-feeding subwebs. The naticids are commonly top predators of these food webs. The replacement of tellinid bivalves typical of the *Syndosmya* Community by the spatangoid echinoids may be due to some environmental factors; local sedimentation rate or redox potential at the sediment-water interface and just below it may be involved here. Recently, Taylor (1971) described communities of this type from the seaward side of mangrove fringes in the western Indian Ocean. Most members of these communities live infaunally. Among the dominant taxa there are deposit feeders, suspension feeders, scavengers (*Nassa*), in-sediment predators (*Natica*), and a few browsers. Each gross ecological niche is dominated by a single species or at most a few ones. Nevertheless, the taxonomic diversity is fairly high due to the income of organisms from adjacent communities. The density of benthic animals is high. The sediment surface is often covered by patches of green algae but beneath the surface the conditions are usually reducing.

Typical *Syndosmya* Communities are known in the fossil record at least since the Paleogene time. Hecker & *al.* (1962, 1963) described from the Fergana Basin benthic assemblages dominated by the tellinid, nuculid, and corbulid bivalves. This association inhabited very soft bottoms in very quiet, poorly oxygenated waters. Báldi (1973) reported the *Nucula-Angulus* community strongly resembling the Recent *Syndosmya* Community; in the Oligocene of Hungary this community occurs in clays and mudstones exceptionally rich in plant debris. The Pleistocene estuarine-lagoonal assemblage of South Africa (Tankard 1975) may represent a community intermediate between the seagrass and *Syndosmya* community types.

Recently, Fürsich (1977) described from the Upper Jurassic clays and silts of England and Normandy the *Corbulomima* association which may also be paralleled with the *Syndosmya* Community.

TURRITELLID ASSEMBLAGE

The following analysis is based on 4 independent samples (*cf.* Fig. 1 and Tab. 3) which contain almost 1,000 identifiable macrobenthic specimens (in addition, the fragments of lithothamnian colonies are very abundant); hence, the probability of failure to detect a species representing numerically only 0.5% of the assemblage would be less than 0.5% (Dennison & Hay 1967).

The turritellid assemblage is to be recognized (*cf.* Fig. 4) by high abundance of the lithothamnia which are absent from all the samples outside this assemblage; the turritellids occur in large amounts exclusively in this assemblage. In addition, some low-fidelity taxa are typically associated with the turritellid assemblage and attain their maximum abundances herein (*Ringicula auriculata buccinea, Odostomia, Anadara diluvii,* and *Turbonilla*). Abundances of *Venus multilamella marginalis* and *Circulus* are also near their maximum values herein. The distinctness is fairly high; and indeed the similarity of turritellid assemblage to the other Korytnica assemblage is rather low (Fig. 5). The homogeneity is very high.

As indicated by the factor analysis (Tabs 1 and 4), the turritellid assemblage inhabited soft and fluid bottom in a shallow-water, high-energy environment. The water was relatively clear, marine plants were absent, and the bottom deposit was rather poor in organic matter. The substrate was muddy (Fig. 6). The sediment contains more silt-sized particles in the areas where lithothamnian fragments are more abundant; this reflects probably an increase in the carrying capacity of water. The associated foraminiferal assemblage is significantly impoverished, mostly stunted, and dominated by only two species, namely *Ammonia beccarii* and *Florilus boueanus;* hence, it was recently postulated to represent oligohaline conditions (Walkiewicz 1975, Fig. 5). This assemblage may, indeed, indicate that salinity conditions were restrictive. However, as shown by Clarke & Keij (1973), similar foraminiferal assemblages live at present in the Persian Gulf in hypersaline coastal lagoons and tidal creek systems. In fact, the foraminiferal assemblages of this type are widely tolerant of fluctuating salinity, and inhabit usually the shallow-water turbulent zones where the intermixing of hypersaline, normal marine, and brackish waters occurs (*cf.* Bradshaw 1957; Phleger 1960; Walton 1964). Hence, it may be concluded that the turritellid assemblage and its associated foraminiferal assemblage inhabited shallow-water muddy flats nearby some rocky thresholds settled by the lithothamnia, under conditions of strongly fluctuating water salinity. In such an environment fluctuations in water turbulence and turbidity can also be expected.

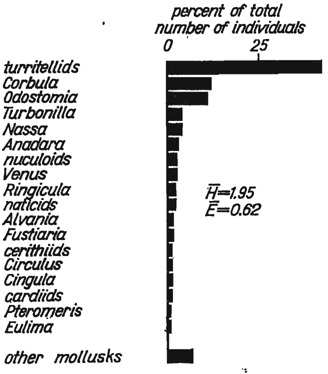


Fig. 31
Average taxonomic composition of the turritellid assemblage

The macrobenthic assemblage is strongly dominated by the turritellids, mainly *Turritella badensis* representing more than 40% of the total number of mollusk individuals. The next positions in the abundance hierarchy are occupied by *Corbula gibba* and *Odostomia* which represent jointly about 20% of the total number of mollusk individuals (Fig. 31). Thus, the numerical dominance is fairly high. In addition to the dominant Korytnica taxa, the actaeonacean gastropods and *Aporrhais* were found in the samples. The abundance of parasitic pyramidellids may indicate that soft-bodied polychaetes were also common. In most samples the bryozoans and fish otoliths occur.

The mollusk diversity of turritellid assemblage is lower than in any of the Korytnica fossil assemblages, except the extreme case of *Corbula* subassemblage. Probably the coefficient is even overestimated since the turritellid assemblage represents a time-averaged assemblage originated under fluctuating environmental conditions. Totally, about 55 macrobenthic species are present in the samples.

The biovolume dominance hierarchy is very similar to the hierarchy in numerical abundance. Thus, the biovolume dominance is very high. In fact, the turritellid gastropods represent about 75% of the total biovolume of preserved macrobenthic taxa. Hence, they are regarded as the single member of trophic nucleus.

The turritellid assemblage consists mainly of infaunal animals (Fig. 32). The epifauna is represented mostly by highly mobile parasite *Odostomia* and a few browsing gastropods. The index of trophic uniformity is very high; it reaches the value of 550. Indeed, about 80% of the total biovolume are represented by the lower level suspension feeders (Fig. 33). Thus, the trophic structure was very simple (Fig. 34). It consisted mainly of very simple food-chain composed by the turritellids and naticids; some additional food-chains were formed by the other suspension feeders and parasitic pyramidellids. The deposit-feeding subweb was only of minor importance. It was composed mostly by the scavenger food-chain which shared the predator with the suspension-feeding subweb. The browsing subweb played only a subordinate role in the energy flow. It was probably sustained by eventual growth of blue-green algae.

feeding category	food location	infauna mobile	infauna sessile	epifauna mobile	epifauna sessile
suspension feeders	high in water mass	▨	▨		
	low in water mass	● turritellids Venus Aporrhais cardiids	Corbula Anadara		bryozoans
deposit feeders	sediment-water interface				
	in sediment	nuculoids Fustiaria		▨	▨
browsers	sediment-water interface	▨	▨	cerithiids Circulus Cingula Alvania	▨
predators	in water mass	▨			
	sediment-water interface	▨	▨	Clavatula	
	in sediment	naticids Ringicula Tornatina	▨	▨	▨
scavengers	carrion	Nassa	▨		▨
parasites	host	Turbonilla Pyramidella Eulima		Odostomia	

Fig. 32. Trophic-substrate-mobility niches of the turritellid assemblage

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

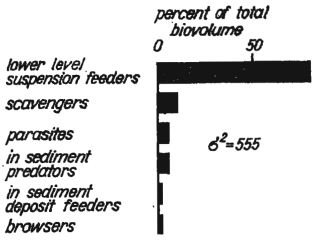


Fig. 33

Dispersion of the biovolume among trophic categories in the turritellid assemblage

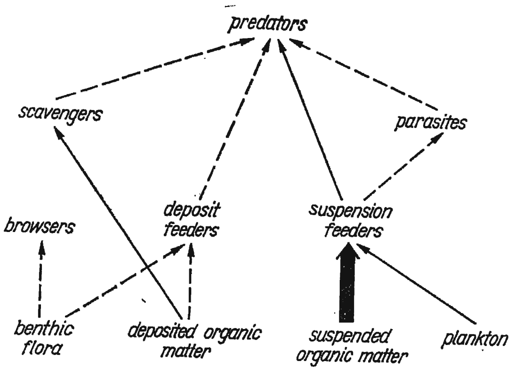


Fig. 34
Simplified trophic web of the turritellid assemblage; width of the arrows indicates relative significance of the paths

This simplicity of the trophic structure resulted from both the restrictive abiotic parameters and highly competitive interactions for space below the sediment-water interface (*cf.* Fig. 35). In fact, densely packed populations of turritellid gastropods make usually the infaunal habitat inaccessible for in-sediment deposit feeders; infaunal sediment-water interface deposit feeders are also repressed by them.

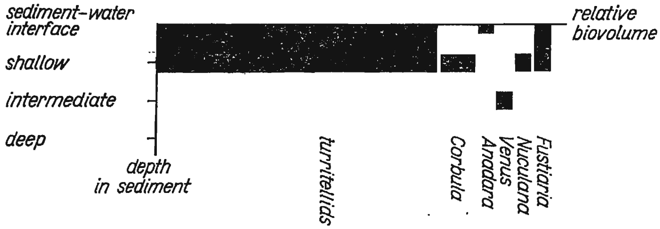


Fig. 35. Spatial relations among the infauna in the turritellid assemblage

Under the conditions of strongly fluctuating physical-chemical parameters (hence, very severe environmental stress), the most profitable appears to have been the *r*-strategy of population growth. Indeed, *Turritella badensis* was distinctly *r*-selected (Hoffman 1976c). The short-term persistence stability of community was probably low but the adjustment stability (*sensu* Margalef 1969) could be very high.

The Recent counterparts of this high-density low-diversity assemblage dominated by the turritellid gastropods are well known to occur on very diverse substrates in protected as well as exposed environments in almost all tropical, subtropical, and temperate-zone seas (*cf.* Ford 1923; Powell 1937; Vatova 1949; Holme 1950; Buchanan 1958; Straaten 1960; Parker 1964; Cadée 1968). They are usually considered as variations of the *Amphiura* Community of Thorson (1957). In general, their trophic structures are very simple and consist mainly of suspension-feeder food-chains. However, Buchanan (1958) reported a community dominated by *Turritella annulata* but also with a considerable proportion of the browsing gastropod *Cancellaria;* the latter feeds probably upon fine mats of filamentous algae encrusting the exposed adapertural whorls of largely sessile turritellids. The infaunal diversity of these communities is mostly controlled by competitive interactions for space.

The turritellid-dominated assemblages are recorded already in the Lower Cretaceous of the United States where they occur mainly in the sandy deposits of middle shoreface environments (Scott 1970, 1974). In these Cretaceous communities the turritellids were usually accompanied by either the cardiid or trigonioid bivalves, that is by semi-infaunal rapidly burrowing suspension feeders, which may indicate that water turbulence and bottom-microrelief variability were fairly high. The ecological structure of these early turritellid communities was somewhat different from that of the Cenozoic ones. The Cretaceous communities appear to have been more species-diverse and less densely packed; the degree of competition for space was probably low; the in-sediment predators were lacking. Hecker & *al.* (1962, 1963) described the Paleogene *Turritella* associations from the sublittoral clays and muddy sands of the Fergana Basin. These associations consist normally of dense turritellid populations, sometimes with minor proportions of naticid gastropods and suspension-feeding bivalves. Very similar benthic assemblages were also reported from the Eocene of California (Givens 1974), Oligocene of Hungary (Báldi 1973), Pliocene of Italy (Robba & Ostinelli 1975), and Pleistocene of Chile (Herm 1969). They lived on either sublittoral clayey bottoms or unprotected sandy substrates.

PTEROMERIS-CORAL ASSEMBLAGE

This assemblage is represented by a single sample (1 in Fig. 1; *cf.* also Tab. 3) taken in the lowermost part of the accessible section of the Korytnica Clays.

The *Pteromeris*-coral assemblage is to be recognized (*cf.* Fig. 4) by very high abundances of six high-fidelity taxa, namely *Limopsis anomala, Dentalium* sp. div. (mainly *Dentalium badense*), solitary corals (mainly the flabellids), *Phacoides agassizi, Clavatula,* and *Pteromeris scalaris.* In addition, some low-fidelity taxa attain their maximum abundances herein. The distinctness is very high; similarity to the other Korytnica assemblages is very low (Fig. 5).

As indicated by the factor analysis (Tabs 1 and 4), in the biotope of this assemblage the water was clear and quiet; the sedimentation rate was low. Marine plants were generally absent; however, the presence of some browsing gastropods, such as *Alvania* or *Architectonica,* may indicate that benthic algae occurred although in minor proportions. The bottom deposit was firm and relatively poor in organic matter. The substrate was purely clayey (Fig. 6).

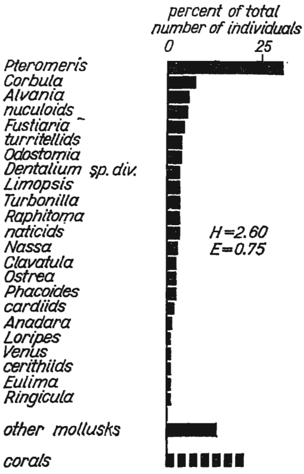


Fig. 36
Taxonomic composition of the *Pteromeris*-coral assemblage

The assemblage is dominated in number by *Pteromeris scalaris* which represents some 30% of the total number of mollusk individuals, and the solitary corals (Fig. 36). The mollusk diversity is high. In addition to the macrobenthos, the foraminifers are very abundant. The fish otoliths and teeth also occur.

The biovolume dominance is fairly high. The corals, *Clavatula,* and *Pteromeris scalaris* are here regarded as the members of trophic nucleus.

feeding category	food location	infauna		epifauna	
		mobile	sessile	mobile	sessile
suspension feeders	high in water mass	▨	▨	pectinids	bryozoans
	low in water mass	● Pteromeris turritellids Phacoides Limopsis Venus cardiids Loripes	Corbula Anadara		
deposit feeders	sediment-water interface				
	in sediment	Dentalium sp.div. nuculoids Fustiaria		▨	▨
browsers	sediment-water interface	▨	▨	Alvania Architectonica	▨
predators	in water mass	▨			● corals
	sediment-water interface	▨	▨	● Clavatula Raphitoma Columbella Genota	
	in sediment	naticids Ringicula	▨	▨	▨
scavengers	carrion	Nassa	▨		▨
parasites	host	Turbonilla Eulima Pyramidella		Odostomia	

Fig. 37. Trophic-substrate-mobility niches of the *Pteromeris*-coral assemblage
Cross-hatched blocks indicate niches not normally occupied by marine benthic animals; taxa marked by black circles indicate members of the trophic nucleus

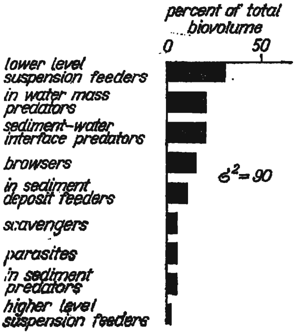


Fig. 38
Dispersion of the biovolume among trophic categories in the *Pteromeris*-coral assemblage

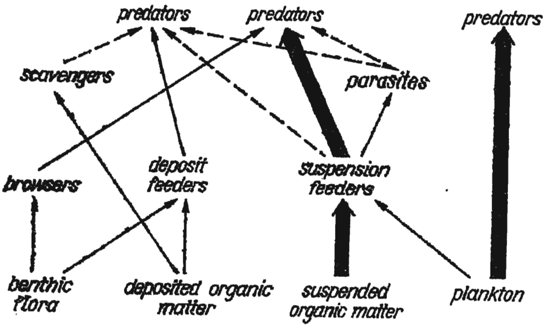


Fig. 39
Simplified trophic web of the *Pteromeris*-coral assemblage; width of the arrows indicates relative significance of the paths

The *Pteromeris*-coral assemblage includes a fairly wide variety of general adaptive types (Fig. 37). In terms of adaptive and feeding types it is distinctly heterogeneous (Fig. 38). In fact, the index of trophic uniformity is only 90; that is it attains its minimum value of the whole Korytnica Clays. Despite such a low trophic uniformity of the assemblage, the trophic structure was significantly less complex and integrated than in the *Turboella-Loripes* community. It consisted mainly of two largely independent subwebs (Fig. 39). One of them was composed exclusively by plankton-eating corals. The other was composed by a few suspension-feeder food-chains dependent mainly upon the predation by pleurotomid gastropods. Both the deposit-feeding and browsing subwebs were markedly less important.

Fig. 40. Spatial relations among the infauna in the *Pteromeris*-coral assemblage

All the dominant infaunal animals lived at approximately the same depth in the sediment (Fig. 40). Nevertheless, their density was probably too low to induce a significant competition for space.

Benthic assemblages strikingly similar in their taxonomic composition and ecological structure to the *Pteromeris*-coral assemblage are well known to occur in the Miocene marine clayey facies. Indeed, as pointed out by Báldi (1961), they are typical of the Baden Clay of the Vienna Basin, Szokolya Clay of Hungary, and deposits exposed at Kostej and Lapugy in the Transylvanian Basin, Rumania. They are always dominated by the extremely abundant and diversified pleurotomids. Infaunal suspension feeders are represented by largely sessile animals. Solitary corals and epibyssates are also fairly common. The proportion of in-sediment deposit feeders is usually low; however it appears to be inversely related to the abundance of corals, which may indicate that it depends strongly upon the local sedimentation rate. Browsers are almost absent, which demonstrates that these communities inhabited environments below the zone of intense light penetration. One may also postulate that the *Turritella spirata* and *Limopsis anomala* community of Bulgaria (Kojumdgieva 1976) represents the same community type. Báldi (1973) paralleled the *Hinia-Cadulus* community from the Oligocene of Hungary with these Miocene deep-sublittoral communities. Presumably, the Cretaceous *Limopsis* association described recently by Kauffman (1976) from the deep-sea Atlantic cores, may also be related to the same community type.

The present-day communities of this type were reported from the Gulf of California (Parker 1964) and the central part of the Persian Gulf (Clarke & Keij 1973). The California community lives at depths exceeding 120 meters. On the other hand, the Persian Gulf community inhabits much shallower waters; it was recorded at depths of some 30—40 meters. Probably, the sedimentation rate and light intensity exert a more significant control over the distribution of these communities than does the bathymetry itself; the degree of substrate firmness may also be involved here.

OSTREA ASSEMBLAGE

This assemblage is represented by a single sample (26 in Fig. 1; *cf.* also Tab. 3) taken nearby the rocky island described by Radwański (1964, 1969, 1970). However, an almost identical assemblage was also reported from the oyster shell-bed in the northern marginal part of the basin (Friedberg 1928, 1931; Kowalewski 1930). Because of the sample singularity, all the following analysis is only an approximation.

The *Ostrea* assemblage is to be recognized (*cf.* Fig. 4) by very high abundance of the oysters. In addition, some other taxa attain their maximum abundances herein. The abundant foraminiferal assemblage is dominated by the miliolids; however, the elphidiids, amphisteginids, heterosteginids, and cibicidids are fairly common (Walkiewicz 1975, Fig. 3). Distinctness of the assemblage is high; its similarity to the other Korytnica assemblages is very low (Fig. 5).

As indicated by the factor analysis (Tabs 1 and 4), the biotope of *Ostrea* assemblage was characterized by very clear and turbulent waters. The bottom deposit contained relatively large amounts of sand-sized and gravel-sized particles (Fig. 6). In fact, Radwański (1969) demonstrated that this was an unprotected onshore environment.

In such environments a high degree of post-mortem alteration of the community composition and structure is to be expected. The *Ostrea* assemblage appears to consist, indeed, of taxa which lived in adjacent habitats. Therefore, the ecological structure was not studied in detail. One may only postulate that some populations inhabited the abrasion surface, whereas the others inhabited muddy substrate in the shallow sublittoral zone; presumably, the kelp and/or seagrasses flourished on the sublittoral flats (*cf.* Radwański 1974).

NERITINA-NASSA-MELANOPSIS ASSEMBLAGE

Radwański (1969, 1974) reported from the southern marginal part of the Korytnica basin still another fossil assemblage. However, it occurs only in a few small isolated patches (asterisked in Fig. 1), and has not been detected in the course of the present study.

Perfunctory analysis of the paleontological collections indicates that distinctness of this assemblage is very high. The assemblage is strongly dominated in both number and biovolume by a few mollusk taxa, most of which are absent from the other Korytnica assemblages. Among the most common taxa there are the gastropods *Neritina, Nassa schoenni, Melanopsis, Turritella erronea, Turritella dertonensis, Terebralia,* and *Natica pseudoredempta.* The fossil density is very high. Both the taxonomic diversity and trophic complexity are very low. The trophic web was composed by very short and simple food-chains.

This ecological structure resembles very closely that of the present-day communities inhabiting poorly oxygenated mangrove swamps (*cf.* Macnae & Kalk 1962a; Macnae 1963; Parker 1964; Taylor 1970, 1971; Braithwaite & *al.* 1973). This interpretation was also suggested by Radwański (1974).

Similar benthic assemblages are well known to occur as allochthonous assemblages in the so-called „detrital Sarmatian" formation of southern Poland (*cf.* Radwański 1973). Moreover, Bałuk (1970) recorded a similar indigenous assemblage in the clays at Niskowa (layers *2* and *3*). The *Polymesoda-Tympanotonus* community described by Báldi (1973) from the Oligocene of Hungary may also represent the same community type.

ECOLOGICAL SUCCESSION

When introducing a conceptual model of benthic marine communities, Johnson (1972) pointed out that in shallow-water ecosystems small-scale physical disturbances occur almost continuously; some disturbances appear random, others occur periodically and in a rather predictable manner. Therefore, nearbottom gross environments are fairly heterogeneous although the environmental gradients tend to be low. On the other hand, distant parts of benthic communities are largely independent of one another because the biological interactions among benthic animals occur mostly over very short distances. Under such conditions, spatial heterogeneity of gross environments leads to partitioning communities into several more or less discrete subcommunities individualized in response to local environmental parameters. Thus, shallow-water benthic communities can be justifiably considered as possessing a spatially mosaic structure.

Johnson (1972) postulated also that any physical disturbance that actually affects a community composition will downgrade the community to an earlier stage in the ecological succession. Ecological succession is here regarded as a short-term orderly directed process of biologically controlled changes in community structure and composition; it takes place in a constant gross environment, begins at a pioneer colonization stage, and leads ultimately to attainment a climax stage (all pre-climax seral stages are thought to be immature and unstable); it is usually assumed that as the maturity of an ecosystem is achieved through the ecological succession, the taxonomic diversity, niche specialization, trophic complexity, and proportion of characteristic (equilibrium) species increase, while the net production and proportion of ubiquitous (opportunistic) species decrease (*cf.* Whittaker 1953; Margalef 1968; Odum 1971). Then, the nature of shallow-water benthic communities can be recognized as that of a spatio-temporal mosaic, parts of which are at different seral stages (Johnson 1972). If so, an order of ecological succession can be correctly reconstructed from the lateral as well as vertical relationships among the samples.

However, it may be very difficult to recognize whether a set of paleoecological samples changing continuously in their composition from one endmember to another one, does actually reflect ecological succession or community replacement. The latter term designates a process of physically controlled ecological reorganization taking place in a significantly changing gross environment, and leading ultimately to the replacement of one ecologically mature community by another mature community (Boucot 1975; Hoffman & Narkiewicz 1977). In a changing environment adjacent communities (*i.e.*, intergrading communities of Johnson 1972) are obviously most likely to replace one another. Hence, in a sense, both ecological succession and community replacement grade into each other, acting at the same place and time. Moreover, a physical disturbance does not always degrade community to an earlier seral stage but sometimes may permit the attainment of a new stage, resulting in the organization of another ecological structure (*cf.* Bretsky & Bretsky 1975). Nevertheless, community replacement and ecological succesion represent quite different phenomena and are to be distinguished whenever possible.

In fact, this may be accomplished by means of a detailed structural analysis of endmember samples, since the process of community replacement appears to consist of two distinct although intergrading in time phases (*cf.* Johnson 1972). Firstly, physical perturbations downgrade the community inhabiting a given area. Secondly, characteristic species of another community begin to appear accordingly to the order of ecological succession, and successively the new community achieves its mature stage. Thus, in general, ecological succession should be reflected by a set of samples changing in their composition from a low-complexity extreme to high-complexity one; whereas in a record of community replacement both endmembers should represent highly complex ecological structures (however, the effects of differential complexities among communities must also be taken into account).

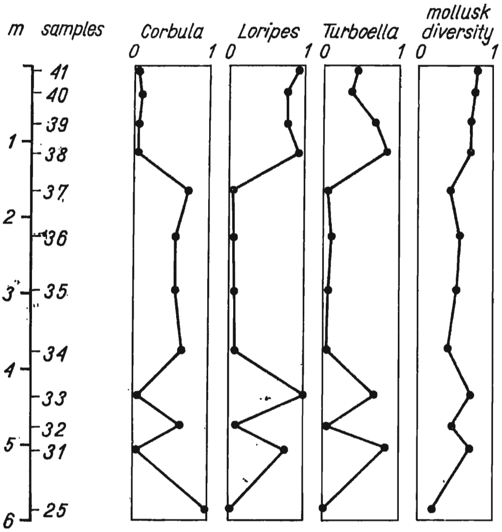


Fig. 41
Oscillatory changes in taxonomic composition (relative abundance of three dominant taxa, and mollusk diversity) of the Korytnica assemblage through time

The samples from within the *Corbula* and *Turboella-Loripes* assemblages change almost continuously from the extreme *Corbula* subassemblage to the other extreme of *Turboella-Loripes* subassemblage. In fact, along this abstract axis the numerical proportion of *Corbula gibba* decreases from some 80% to less than 10%, whereas the numerical proportions of *Loripes dentatus niveus* and *Turboella* increase each from 0 to almost 20%. Parallel changes in abundance occur in most other dominant taxa. Because of the lack of any isochronous surface, the samples must be regarded as spatio-temporally different subcommunities. Nevertheless, a dozen of these samples were taken approximately along a vertical section (*cf.* Fig. 1), which allows to suspect oscillatory changes in taxonomic composition through time (Fig. 41). All the samples from within the *Corbula* and *Turboella-Loripes* assemblages were taken in the central part of the basin. Thus, it may be concluded that this area was inhabited by a spatio-temporal mosaic composed of either two intergrading communities, or a single community undergoing ecological succession and degradation in response to local environmental changes.

The above presented analyses of the ecological structure of Korytnica fossil assemblages demonstrate clearly that ecological complexity was much higher in the *Corbula*-scaphopod subcommunity than in the *Corbula* subcommunity. It was still higher in the *Turboella-Loripes* community. This major trend is evident in taxonomic diversity (Figs 9, 16, and 17) as well as in variety of general adaptive types (Figs 10, 18, and 19) or complexity of trophic web (Figs 13, 22, and 23). Therefore, the spatio-temporal mosaic of samples from within the *Corbula* and *Turboella-Loripes* assemblages can be most likely interpreted as reflecting the ecological succession leading from an initial colonization of a barren muddy substrate to development of a mature seagrass community. Temporary degradations of the community, reflected by the oscillatory changes in composition between the extremes of *Corbula*-scaphopod subassemblage (that is late *Corbula* seral stage) and *Turboella-Loripes* subassemblage (that is late *Turboella-Loripes* seral stage) may have resulted from such local environmental disturbances as an increase in water turbulence, turbidity (causing a drop in light penetration), or sedimentation rate. These factors could act upon the algal epiphytocoenoses and associated macrobenthos rather than upon the seagrasses themselves. However, the *Corbula* subassemblage (that is early *Corbula* seral stage) represents probably an almost completely barren substrate; hence, its periodical occurrence in the Korytnica Clays may indicate that sometimes the seagrasses were also killed.

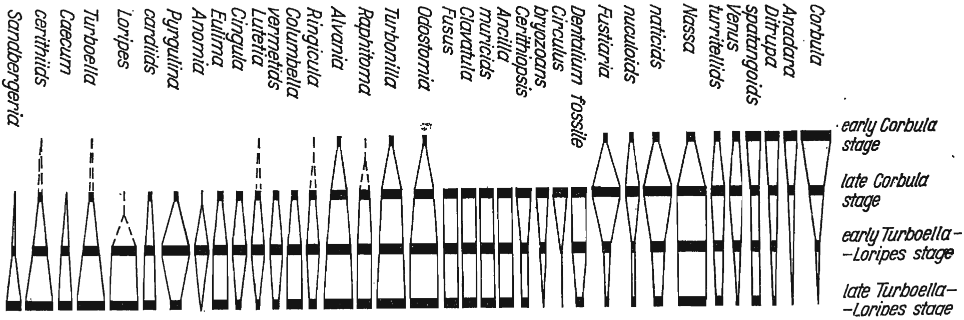


Fig. 42. Ecological succession in the bay-center ecosystem; for each taxon changes in its relative abundance at successive seral stages are shown

The order of ecological succession in the Korytnica seagrass community can be briefly summarized as follows (Fig. 42): At first, a barren muddy substrate is colonized by *Corbula gibba* accompanied by *Anadara diluvii, Ditrupa cornea,* and the spatangoid echinoids; *Venus multilamella marginalis,* the turritellids, *Nassa,* and the naticids also occur at the early *Corbula* stage although they attain their maximum abundance later. Thus, the pioneer colonization stage is dominated by *r*-selected suspension feeders with some *K*-selected predators and scavengers in minor proportions. These pioneer suspension feeders are largely sessile and able to efficiently stabilize the bottom. In fact, such a function of the pioneer community was also observed by Rhoads (1975) on recently depopulated subtidal muddy bottoms of Buzzards Bay and Long Island Sound, United States. These pioneer populations nourish their own habitats by supplying large amounts of deposited organic matter, which allows the scavengers and deposited-detritus feeders to significantly increase in abundance. At the same time diverse predators and parasites appear. The browsers also attain considerable abundances indicating that at the late *Corbula* stage marine plants settle the environment. In general, the proportions of suspension feeders and deposit feeders decrease at the early *Turboella-Loripes* stage; anyway, the pioneer suspension feeders are successively replaced by those able to resist low oxygen capacity and those living epiphytally. The browsers appear in very large amounts indicating that at this seral stage the community represents already a true seagrass community. All the predators and parasites persist but among the latter group *Pyrgulina interstincta* becomes dominant. The late *Turboella-Loripes* stage is dominated by diversified browsers, the small lucinoid suspension feeders, and unusually diverse high trophic-level consumers. Nevertheless, the overall ecological complexity seems to drop a little when compared to the earlier seral stage, just as it occurs commonly at the climax stage (*cf.* Margalef 1963; Odum 1971; Bretsky & Bretsky 1975). This ecological trend seems to be explicable in terms of general properties of complexity.

In fact, it was often argued that contrary to the general consensus among ecologists, large randomly connected systems have a decreased probability of being stable as the number of connections in the system increases (Hairston & *al.* 1968; Gardner & Ashby 1970; May 1972, 1973). Nevertheless, Angelis (1975) proved that stability of a food-web model increases with the increase of connectance, that is probability of realization all web connections possible, and it begins to decrease only when connectance is great enough (greater than 0.5). This critical value would probably be somewhat higher if non-linearity of many biotic interactions taken into account (*cf.* Smith 1975). Then, the decrease in ecological complexity at the latest stage of a succession would indicate that equilibrium connectance of the ecological structure was overcome, that is stability of the community was endangered.

At virtualy all stages of this succession the Korytnica community was composed by both *K*-selected and *r*-selected populations. This contradicts the common assumption that under conditions of environmental predictability and/or ecological maturity, communities consist mainly of *K*-strategists, whereas *r*-strategists dominate at early seral stages and/or in highly unstable physical environments (Levinton 1970; Hallam 1972; Rollins & Donahue 1975; Walker & Alberstadt 1975). In fact, Surlyk (1972), Stump (1975), and Walker & Parker (1976) presented some evidence that the so-called time-stability hypothesis of Sanders (1968, 1969) may be unjustified, at least in its part concerning with strategy of population growth.

The analysis of mortality patterns of Korytnica dominant mollusk populations may indicate that *r*-strategy is required from populations living in environments far from their ecological optimum; that is under conditions unfavorable with respect to any dimension of their prospective niche, be it biotic or abiotic. Under more favorable environmental conditions the same populations or at least some of them can be expected to become resource-limited. As the matter of fact, such a flexibility in mortality pattern of populations was postulated by Slobodkin & Rapoport (1974). Then, the choice of anyone of the population-growth strategies seems related notasmuch to the environmental predictability and/or ecological maturity as to the whole of a population relationships with its biotic and abiotic environment (Hoffman 1976c).

Some communities inhabiting marginal parts of the Korytnica basin (namely, the turritellid and *Corbula*-spatangoid assemblages) were strongly dominated by the taxa occurring very early in the order of the above described ecological succession. This may suggest that these marginal communities can develop directly from the early *Corbula* seral stage. An external, physical disturbance of fairly long duration could stimulate organization of an entirely new ecological structure which attained a steady state due to some environmental as well as purely biological factors (for discussion of a similar phenomenon *see* Bretsky & Bretsky 1975).

RECONSTRUCTION OF ENVIRONMENT

The results of the present synecological study of the Korytnica macrobenthos allow further refinement of the knowledge of environmental conditions in the Korytnica basin.

Most benthic communities inhabiting the Korytnica basin seem to have been almost identical in their ecological structure with the Recent communities of tropical or subtropical seas, especially of the Indian Ocean. Tropical-zone conditions are also indicated by the exceptionally high taxonomic diversity of mollusks (*cf.* Fischer 1960; Stehli & *al.* 1967; Schopf 1970). Thus, the synecological study supports the inference about tropical or subtropical conditions in the Korytnica basin (and by implication in the Polish Miocene) which followed the previous paleontological investigations (Bałuk & Radwański 1967; Bałuk & Jakubowski 1968; Bałuk 1971, 1972, 1975; Radwański 1969, 1974, 1975).

The Indian affinities of the Korytnica organisms and benthic communities suggest that the intercommunication between the Tethyan (and Central-Paratethyan) and Indo-Pacific provinces persisted throughout the early and middle Miocene although possibly with some interruptions (*cf.* Radwański 1974, 1975). In fact, this is confirmed by the co-occurrence of the Indo-Pacific colonist *Borelis melo* and the East-American colonist *Miogypsina globulina* in the Miocene deposits of Iraq (Čtyroký & *al.* 1975).

When the common occurrence of the *Pteromeris*-coral assemblage in the lowermost, clayey part of the Korytnica Clays (Bałuk 1974, oral communication) taken into account, the present study indicates that the facies development of the Korytnica basin agrees well with the model of maturation of coastal bays and lagoons (*cf.* Barnard 1970; Warme 1971). As the matter of fact, the *Pteromeris*-coral community lived below the euphotic zone, whereas all the other Korytnica assemblages indicate clearly the conditions of intense light penetration. Under conditions of high terrigenous influx, light intensity appears to decrease very rapidly with depth (Purser & Seibold 1973), which allows benthic communities of *Pteromeris*-coral type to live at depths of some 30—40 meters or even less. Then, the other communities of the Korytnica Clays can be postulated to have lived at depths of a dozen or so meters. The overlying Heterostegina Sands appear to represent still shallower-water deposits and biota, thus indicating that the basin became filled with sediment up almost to the sea level (*cf.* Radwański 1969, 1970, 1974).

At the stage of *Pteromeris*-coral fauna the basin was relatively deep; the low-energy clear-water conditions allowed low sedimentation rate. Therefore, the habitat was highly stable and predictable in ecological time. On the other hand, it persisted for a fairly long period of time until the deposition controlled mainly by terrigenous influx made the basin shallow enough to allow settlement by the seagrasses. However, once this had been possible, the bay center became covered with a more or less dense seagrass population. Then, the immigrated seagrasses accelerated the deposit accumulation by trapping sediment particles; hence, they were leading to destroy their own biotope by successive filling the basin up. Among the seagrass blades the salinity, pH, and oxgygen capacity fluctuated in a variable manner. Thus, neither ecological stability, nor predictability of the habitat was very high. In the marginal parts of the basin (*cf.* Radwański 1969, 1974) the mangrove marshes and fore-mangrove poorly oxygenated shelters occurred. One may postulate that as the basin became more and more mature, these nearshore environments moved successively to the bay center, diminishing the basin volume (*cf.* Barnard 1970; Warme 1971). In fact, this would explain the occurrence (although sparse) of mangrove fauna in the *Corbula* and *Turboella-Loripes* assemblages, while it lacks at all in the *Pteromeris*-coral assemblage. The rocky shores were inhabited by the oyster populations. In the north, the shallow-water muddy flats developed in the neighborhood of Chomentów rocky thresholds settled by the lithothamnian algae (*cf.* Radwański 1969). These flats were inhabited by the dense populations of turritellid gastropods adapted probably to withstand fluctuations in salinity.

With possible exception of the stage of *Pteromeris*-coral fauna, land proximity ensured probably high nutrient supply from outside the Korytnica benthic ecosystem. However, the level of this supply could vary within a fairly broad range, accordingly to climatic conditions; this variation appears to have been rather predictable. On the other hand, the *Pteromeris*-coral community was primarily dependent upon the productivity of overlying water mass, that is upon the plankton, the abundance of which is well known to vary within a very broad range and in a completely unpredictable manner. The productivity of benthic plants was obviously the highest in the *Turboella-Loripes* ecosystem; it was much lower in all the other Korytnica ecosystems. Biomass of benthic plants exhibits usually a strong seasonal variation under temperate-zone conditions (*cf.* Conover 1958) but it can be postulated to be more or less stable under tropical or subtropical conditions. Thus, it may be concluded that in the *Turboella-Loripes* ecosystem the level of trophic resources was very high and stable. It was much lower and completely unpredictable in the *Pteromeris*-coral ecosystem. All the other Korytnica communities dealt with unstable but fairly predictable trophic regimes.

CONCLUSIONS

Taxonomic diversity has usually been considered as an adequate measure of ecological complexity (*cf.* Sanders 1968, 1969; Slobodkin & Sanders 1969; Johnson 1970; Rollins & Donahue 1975; Scott 1975, 1976). The latter term is generally meant to designate total connectance of the web of biotic relations in an ecological structure, that is to embrace both the trophic and spatial interactions. Therefore, the concept of ecological complexity is very difficult (if possible at all) to quantify. So more that the index of trophic uniformity does not adequately reflect trophic complexity of a community, even if it is treated in a very sophisticated manner, that is if a large number of feeding categories is distinguished. Indeed, the Nesis' index does not take into account any feedback in a trophic web, while interactions of this type are fairly common in real communities. Moreover, the concept of ecological complexity should also embrace behaviorally founded specializations. Nevertheless, qualitative analyses of both trophic and spatial structures of communities may allow at least to approximate a hierarchy in their relative complexity. Then, the results of the present study raise the question whether the basic assumption of ecological significance of taxonomic diversity is valid or not.

In fact, in the Korytnica fossil assemblages the trend in taxonomic diversity can hardly be used to predict the trend in ecological complexity. The former one is obviously biased by selective preservation and differential mortality patterns and life spans among macrobenthic species. Nevertheles, all the Korytnica assemblages are composed mainly of organisms belonging to the same preservation class of Lasker (1976); therefore, they should be equally affected by the preservation bias. On the other hand, the trend in diversity seems to be identical no matter whether it is determined on the basis of Shannon's uncertainty or simply of total number of species. The hierarchy in taxonomic diversity is as follows (in the decreasing order):

Turboella-Loripes-Pyrgulina-scaphopod subassemblage;
Turboella-Loripes and *Corbula*-scaphopod subassemblages;
Pteromeris-coral assemblage;
Corbula-spatangoid assemblage;
turritellid assemblage;
and extremely low-diversity *Corbula* subassemblage.

The hierarchy in ecological complexity is as follows (in the decreasing order):

Turboella-Loripes assemblage;
Pteromeris-coral assemblage;
Corbula-spatangoid assemblage;

Corbula-scaphopod subassemblage;
Corbula subassemblage and turritellid assemblage.

This discrepancy between the hierarchies in taxonomic diversity and ecological complexity may suggest that these two community characteristics are independent of each other (*cf.* also Ashton & Rowell 1975; Moldenke 1975).

Indeed, this conclusion is not unexpected when the feasibility of relaxation an interspecific competition in different portions of even highly integrated ecosystems taken into account. Thus, a decrease in salinity is intolerable for protobranchiate deposit-feeding bivalves and hence, it may cause a decrease in diversity of deposit feeders; similarly, oxygen defficiency makes the environment inaccessible for most suspension feeders, while high substrate mobility makes the environment unfavorable for sessile suspension feeders. All these excluded species groups may or may not be replaced by other benthic species; nevertheless, in general, a decrease in taxonomic diversity due to such physical controls can hardly be entirely counterbalanced by an immigration of new species or expansion of the modal niche. Under such ecological conditions, some portions of a prospective ecosystem can be expected to remain unrealized. On the other hand, interspecific competition may also be released owing to a superabundance of space or particular food resource.

Both taxonomic diversity and ecological complexity of the Korytnica communities appear also to have been poorly related to environmental stability or predictability. As the matter of fact, the least stable and predictable habitat was settled by relatively low diverse and low complex turritellid community. Nevertheless, the *Corbula* subcommunity was equally low complex and much less diverse, while its habitat appears to have been much more stable and predictable. Probably the biotope of *Corbula* subcommunity was as stable and predictable as those of *Corbula*-scaphopod subcommunity, *Corbula*-spatangoid community, or *Pteromeris*-coral community, although the latter three communities were significantly more diverse and complex than the former one.

On the other hand, the ecological complexity appears to have been almost equal under conditions of low (*Pteromeris*-coral community) and high (*Corbula*-spatangoid community) level of trophic resources. It was the highest in the *Turboella-Loripes* community, that is in the environment having extremely high and relatively stable food supply. This contrasts with the model proposed by Valentine (1971, 1973).

It seems that in the Korytnica basin within-habitat physical-chemical heterogeneity and stress exerted the most strong control over the complexity of macrobenthic communities. Nevertheles, the complexity was probably influenced also by biotic interactions.

In summary, the results of the present study may raise the question of validity of the ecological theory relating basic structural characteristics of benthic communities to environmental stability and/or predictability. As the matter of fact, some evidence that the time--stability hypothesis of Sanders (1968, 1969; *cf.* also Slobodkin & Sanders 1969; Bretsky & Lorenz 1970; Johnson 1970) may be unjustified was already presented by Dayton & Hessler (1972), Gibson & Buzas (1973), Goodman (1975), and Moldenke (1975).

The evidence from the analysis of a few fossil assemblages from the Korytnica Clays cannot obviously falsify ultimately the general ecological theory. So more that the predictions following from the theory cannot be rigorously tested in the fossil record. Therefore, extensive work in this field is needed.

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