

MICHAŁ KOWALEWSKI

A hermeneutic analysis of the shell-drilling gastropod predation on mollusks in the Korytnica Clays (Middle Miocene; Holy Cross Mountains, Central Poland)

ABSTRACT: Shell-drilling predation by naticid and muricid gastropods on mollusks has been studied in the fossil assemblage of the Korytnica Clays (Middle Miocene; Holy Cross Mountains, Central Poland). To this end, the hermeneutic method has been employed, which begins with a pre-understanding of a natural phenomenon, then proceeds with data analysis, thus leading to improved understanding, etc. Three large bulk samples have been analysed, each of them consisting of two spatially adjacent subsamples; these samples cover much of the paleosynecological variability discovered previously in the Korytnica Clays. Sample representativeness analysis did not reject the null hypothesis of subsample identity (and hence sample representativeness) in two of three considered samples; for the third one, its subsamples have been consequently analysed separately from each other. Taphonomic analysis focused on the preservation condition of mollusk shells, left-to-right valve ratio among mollusks, bivalve articulation and gastropod preservation, scaphopod preservation, and size-frequency distribution of a number of species. This analysis leads to the conclusion that fossils experienced only local post-mortem transportation, virtually no chemical dissolution, and very little time-averaging, except for the one nonrepresentative sample. Fossil fragmentation is mostly due to compaction. Prey analysis has largely focused on the bivalve *Corbula gibba* and the gastropod *Nassa hoernesii*, which has been commonly drilled. Predator analysis concerned both naticid and muricid gastropods. Quantitatively, prey-size preference by the predators, drillhole location distributions, and predation efficiency have been studied, whereas some other questions, such as the preference hierarchy of prey species by the predators could be addressed only qualitatively. Beyond the conclusions concerning the fossil assemblage of the Korytnica Clays, the study also points to the inevitable limitations of qualitative paleoecological inference.

INTRODUCTION

Predation by shell-drilling gastropods is among the best documented ecological processes to be found in the fossil record. This is due to their significance in the Late Mesozoic and Cenozoic benthic marine communities (KOHN 1985). Undoubtedly, analysis of the shells drilled by predatory gastropods provides opportunities for a profound qualitative interpretation of paleoecology and even paleoethology of these snails and their prey. Most of the studies accomplished thus far, however, are quantitative, while the researchers

(e.g., TAYLOR 1970, ADEGOKE & TEVESZ 1974, HOFFMAN & *al.* 1974, KOJUMDJEVA 1974, BERG & NISHENKO 1975, THOMAS 1976, TAYLOR & *al.* 1983) quite often ignore the constraints imposed by the very nature of the fossil record.

In this paper, an attempt is undertaken to assess the cognitive value of quantitative paleoecological analysis of predation by shell-drilling gastropods in the Middle Miocene Korytnica Clays; Holy Cross Mountains, Poland. The Korytnica Clays, crop out in the Korytnica Basin, which was the innermost and at least partly isolated area of the Korytnica Bay (*see* RADWAŃSKI 1969, BAŁUK & RADWAŃSKI 1977).

Because of the historical status of a majority of geological disciplines (SIMPSON 1963, ROGERS 1989), including paleontology (MARK & FLESSA 1977; HOFFMAN 1979a, 1981; KITCHELL 1985a), the hermeneutic methodology is employed following the suggestion made by HOFFMAN & REIF (1988). The hermeneutic method assumes that, in order to analyse a phenomenon, its "pre-understanding" is required, since it is impossible to analyse any phenomenon without any prior knowledge about its nature, structure, and relations to the outer environment. In the case of quantitative paleoecology, the pre-understanding comprises an understanding of (i) taphonomic processes in the study area, (ii) the limitations of methodological uniformitarianism, and (iii) ecological processes in the original ecosystem. Data analysis provides then material for a better understanding of the phenomenon and for correction of the pre-understanding.

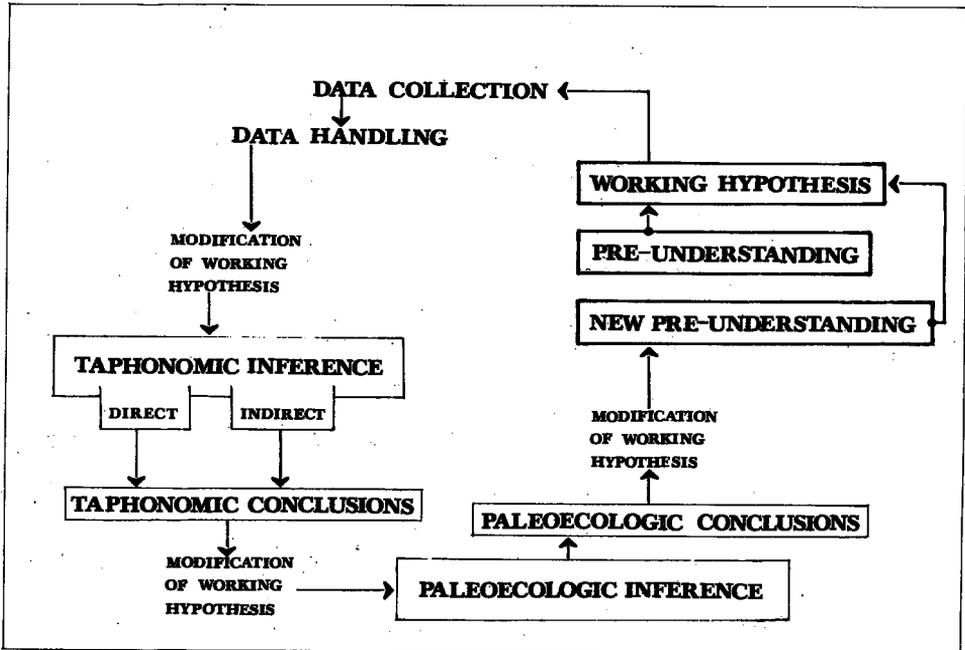


Fig. 1. The analysis of predation by shell-drilling gastropods from the Korytnica Clays — flowchart of hermeneutic methodology

The flowchart of the hermeneutic analysis performed in this work (Text-fig. 1) presents the previous studies on paleoecology of predation by shell-drilling gastropods as the pre-understanding which initially defines the methods and aims of the study. The initial approach is later modified as result of the analysis. This paper bases on an abbreviate and improved version of master's thesis (KOWALEWSKI 1990).

MATERIALS AND METHODS

Three double samples have been collected in 1988-1989 from the Korytnica Clays (Text-fig. 2), the geological setting of which is exhaustively discussed by RADWAŃSKI (1969) and BAŁUK & RADWAŃSKI (1977, 1979, 1984). The sample location has been intended to cover a substantial part of the paleosynecological variability observed in the Korytnica Clays (BAŁUK & RADWAŃSKI 1977; HOFFMAN 1977, 1979b). Sample *I* represents the most typical fossil assemblage of the Korytnica Clays, sample *II* represents the assemblage of clays interfingering with oyster shellbeds, and sample *III* (derived from an area close to the contact between clays and gravels) represents the *Corbula* assemblage of HOFFMAN (1977).

The samples were sieved on a 1-mm mesh, but all specimens smaller than 1.5 mm have been rejected in order to avoid the bias of boundary conditions. Mollusks shells have been identified to the species level only in those taxa with features allowing for proper taxonomic identification even in the case of the smallest specimens. All other shells have been identified to the genus level.

Most of the shell material to be found in the Korytnica Clays is fragmented. Quantitative database should in principle, comprise solely the specimens whose true maximum size can be measured (CUMMINS & *al.* 1986). Adoption of this procedure, however, would leave out of the scope a number of abundant gastropod taxa, such as *Turritella badensis*, *Bittium reticulatum*, *Triphora*, *Eulima*, and *Turbonilla*, since their specimens in the Korytnica Clays generally lack the apertural part. Another criterium must have been adopted for these "trouble taxa". The present author decided to include, for these taxa, all shell fragments that comprise the abapertural part and are twice longer than wide. This criterion is obviously arbitrary, but it has the advantage of avoiding an excessive overestimate of the relative abundance of these trouble taxa.

The specimens have been counted, individual valves being considered each as a half of bivalve specimen (Table 1). They have been measured with ± 1 mm accuracy. Articulated bivalve shells and gastropod shells with preserved protoconch have also been counted. In addition, scaphopod fragments have been counted as an index of shell fragmentation because even their smallest shell fragments are identifiable.

The specimens have been categorized according to their preservation state, with each class being arbitrarily given a numerical value as follows:

- 3.0 — shells perfectly preserved: complete specimens with fully preserved ornamentation, lustrous surface, unabraded edges, and (in the case of gastropods) protoconch;
- 2.5 — shells well preserved: complete specimens with easily discernible ornamentation and edges;
- 2.0 — shells poorly preserved: incomplete specimens with hardly discernible ornamentation and abraded edges, but with features allowing for reconstruction of the actual shell size;
- 1.5 — shells incomplete, of actual shell size unknown.

Gastropod drillholes found in the mollusk shells in the Korytnica Clays belong to *Oichnus paraboloides* and *O. simplex* of BROMLEY (1981), the former being traditionally assigned to the activity of naticids and the latter to that of muricids (*e.g.*, CARRIKER & YOCHELSON 1968, BROMLEY

1981, KITCHELL & al. 1981, HOFFMAN & MARTINELL 1984). The difference has been attributed to the presence of an accessory boring organ in the Muricacea, but not in the Naticacea (CARRIKER 1981). The present author follows the tradition, though a number of caveats are in order. First, recent studies indicate that some naticids (*Naticarius* and *Tectonatica*) also possess an accessory boring organ and their drillholes do not significantly differ from the muricid ones (GUERRERO & REYMENT 1988). Moreover, *O. simplex* gradually passes into *O. paraboloides* in some thin-shelled mollusk taxa (cf. HOFFMAN & al. 1974). Finally at least some naticid species feed on mollusks without shell-drilling (VERMEIJ 1980); these species, however, attack their prey primarily by edge-drilling, while edge-drillings only rarely occur in the Korytnica Clays. [After the completion of the data, ARUA & HOQUE (1989) have presented shell-drilling predation analysis based on detailed morphological study of drillholes. Their methods seems to offer a considerable potential toward resolution of ambiguities in drillhole identification].

Table 1

Abundances of mollusk species from the Korytnica Clays (in the collected samples)

TAXON	SUBSAMPLE					
	Ia	Ib	IIa	IIb	IIIa	IIIb
BIVALVIA:						
<i>Anadara diluvii</i>	42	10	2	7	7	5
<i>Chama gryphoides</i>	0	0	8	8	0	0
<i>Corbula gibba</i>	713	943	106	135	463	350
<i>Cyclocardia scalaris</i>	5	5	71	65	0	0
<i>Linga (Bellucina) agassizi</i>	0	0	0	0	8	4
<i>Limopsis anomala</i>	1	0	2	2	0	0
<i>Lucina</i> sp.	0	0	0	0	0	1
<i>Lutetia nitida</i>	0	0	0	1	0	0
<i>Microloripes dentatus niveus</i>	1	2	0	2	1	4
<i>Myrtea spinifera</i>	0	0	1	0	0	0
<i>Pitar rudis</i>	0	2	0	0	0	0
<i>Ostrea frondosa</i>	0	0	76	75	0	0
<i>Venus multilamella</i>	50	48	5	3	9	0
GASTROPODA:						
<i>Alvania</i> spp.	4	11	75	20	2	0
<i>Bittum reticulatum</i>	9	4	82	39	0	1
<i>Columbella</i> spp.	3	1	11	3	0	0
<i>Eulina</i> spp.	0	0	1	1	1	2
<i>Julubinus caelina</i>	1	0	0	0	0	0
<i>Menesto peculiaris</i>	8	5	0	0	0	0
<i>Nassa hoernesii</i>	242	201	41	22	23	19
<i>Nassa limata</i>	3	8	2	2	1	0
<i>Natica</i> spp.	60	53	25	16	18	24
<i>Neritina picta</i>	1	1	1	0	0	0
<i>Pallia exsculptata</i>	0	0	0	0	0	1
<i>Piramidella</i> sp.	0	0	1	1	0	0
<i>Pyrene subcorrugata</i>	0	0	3	7	0	1
<i>Raphitoma hispidula</i>	15	7	1	1	2	0
<i>Raphitoma plicatella</i>	3	5	14	11	0	2
<i>Ringicula auriculata</i>	31	12	8	11	1	3
<i>Rissoina decusata</i>	0	0	1	0	0	0
<i>Rissoina podolica</i>	0	0	0	1	0	0
<i>Scala spinosa</i>	5	1	0	0	0	2
<i>Triphora perversa</i>	0	1	2	1	0	0
<i>Turbonilla</i>	1	0	0	1	0	0
<i>Turricula</i> sp.	0	0	0	0	0	1
<i>Turritella badensis</i>	32	21	25	9	7	2
<i>Turritella bicarnata</i>	0	0	1	0	0	0
SCAPHOPODA	13	9	7	13	7	2

Drillhole location has been recorded for each specimen. In bivalves, the shell has been arbitrarily divided into sectors (Text-fig. 3b). In gastropods, a modified method of BERG & NISHENKO (1975) has been adopted (Text-fig. 3a). Drillhole diameter has been measured with ± 0.1 mm accuracy, with all regenerated and incomplete (*sensu* KITCHELL & *al.* 1986) borings counted.

For each mollusk taxon, biomass has been calculated by the empirical equation introduced by POWELL & STANTON (1985; *see also* STAFF & *al.* 1985, 1986; CUMMINS & *al.* 1986).

SAMPLE REPRESENTATIVENESS

Quantitative analysis demands representative samples, and this condition can only be met if the rules of element distribution within the investigated population are at least partly known (BARNETT 1974). No universal model can be developed for paleoecological study, however, because of the variability in historical conditions. Therefore the present author took double samples from

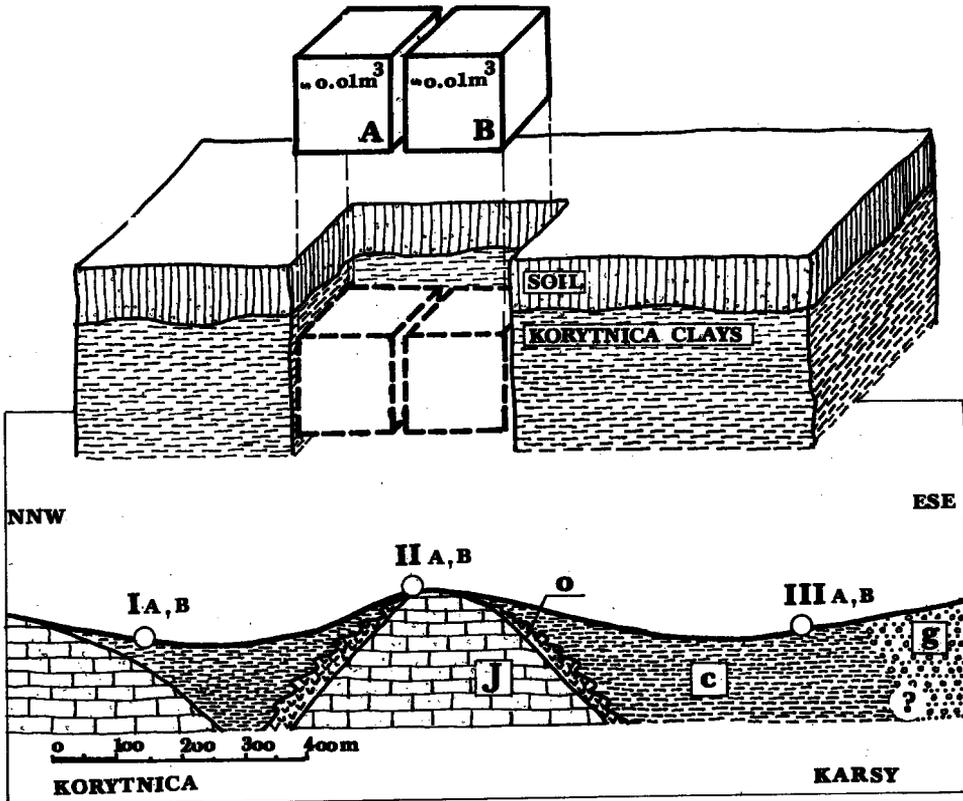


Fig. 2. Idealized cross-section through the central part of the Korytnica Basin, and block-diagram illustrating the method of double-sampling

J — Jurassic substrate, c — Korytnica Clays, o — oyster shellbeds, g — Tertiary gravels (question mark symbolizes unrecognized contact between Tertiary gravels and Korytnica Clays)

each sample location (Text-fig. 2). Since the Korytnica Clays lay horizontally each couple of subsamples are coeval. Since the samples derived from sedimentologically uniform strata, the autochthonous fossils found in each couple of subsamples are most likely to have been sympatric, for it is hardly believable that significant environmental differences existed at a distance of half a meter. Hence paleoecological differences within each couple of subsamples should be insignificant.

There is no basis for statistical evaluation of sample representativeness because there is no data on the expected distribution and the number of degrees of freedom is 1. Therefore, a similarity analysis has been employed to evaluate this postulate, using the data given in Table 1 and a coefficient given by the following formula (cf. COLBATH 1985, SPRINGER & BAMBACH 1985):

$$S = 2(\sum \min(P_{ij}, P_{ik}) / \sum (P_{ij} + P_{ik}))$$

where j, k are subsamples and P is the proportion of i -th species in subsample, and S similarity coefficient.

Since the samples differ in either biofacies (sample *I* and *III* as compared to sample *II*), or fossil concentration (sample *II* and *III* as compared to sample *I*; see KIDWELL 1986 for environmental implications), the similarity coefficient S between subsamples of the same samples should always be higher than the similarity coefficient $S\beta$ between any two subsamples of different samples. Hence, the minimum similarity coefficient ($S\alpha$) within any sample which would allow to consider it as representative equals the maximum $S\beta$.

As shown in Text-fig. 4, this analysis does not allow to reject the null hypothesis that the samples are representative for samples *I* and *III*. Sample *II*, however, is not representative according to this criterion. Therefore, its subsamples are analysed independently.

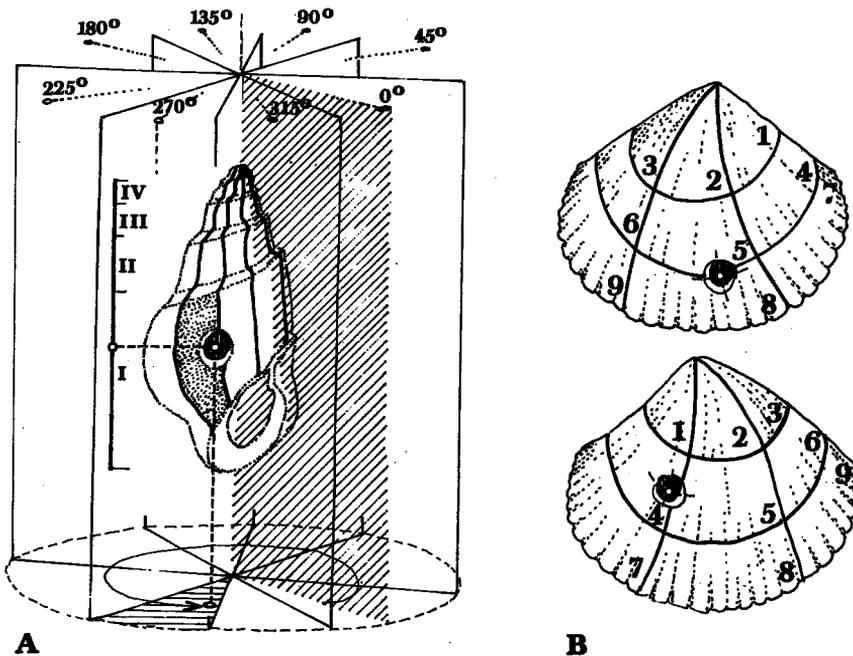


Fig. 3. Methods for measuring drillhole position: A — in gastropods, B — in bivalves

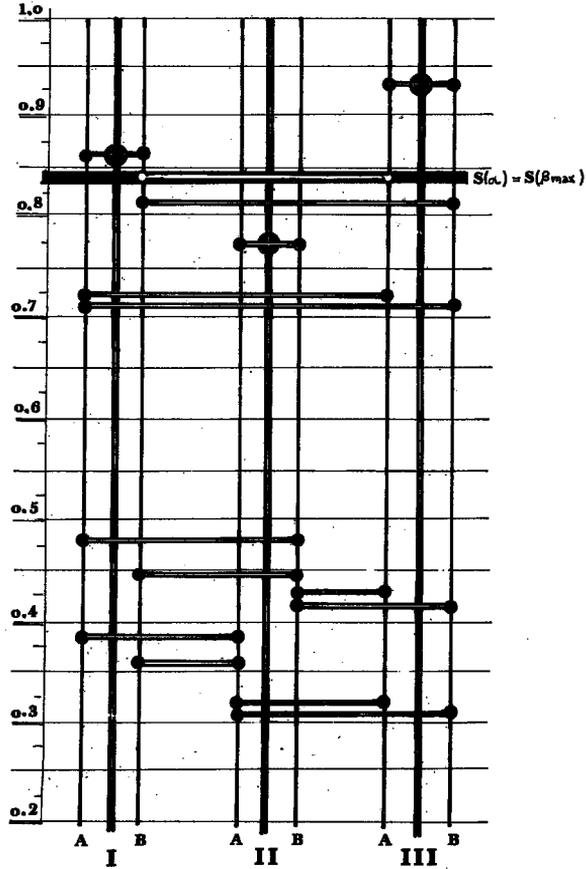


Fig. 4
Samples representativeness; detailed explanation in the text

TAPHONOMY

PRE-UNDERSTANDING

In spite of very intense paleoecological work on the fossil assemblage of the Korytnica Clays, including some quantitative analyses (e.g., HOFFMAN & al. 1974; HOFFMAN 1976a, b, 1977, 1979b; SZCZUCHURA 1987), taphonomy of the Korytnica assemblages has thus far been referred to only marginally (e.g., BAŁUK & RADWAŃSKI 1977, 1979, 1984; HOFFMAN 1976a, 1977; FÖRSTER 1979).

The taphonomic pre-understanding can be summarized as follows:

Fossil distribution is patchy, with fossils concentrated in streaks or lenses. Post-mortem transportation of fossils was at most local, with larger shells often acting as sedimentary traps for juvenile ones (cf. BAŁUK 1971, 1975; JAKUBOWSKI 1972; BARCZYK & POPIEL-BARCZYK 1977). Shell fragmentation was caused by pagurid crabs, but mostly by compaction. Rate of sedimentation and fossil burial was variable. There are virtually no traces of chemical dissolution of fossils. Generally, post-mortem alteration of the assemblage was at minimum.

DIRECT TAPHONOMIC INFERENCE

The above-summarized taphonomic pre-understanding stems almost entirely from qualitative observations and quite nonrigorous inferences. Therefore, the present author undertook a more rigorous analysis of a variety of lines of evidence.

Perfectly and well preserved shells prevail in the samples I and III, while poorly preserved shells, often with chalky surface (*sensu* FLESSA & BROWN 1983) and abiotic perforations, abound in subsamples IIa and IIb (Text-fig. 5). These data indicate a significant difference in intensity of taphonomic processes between I and III, on the one hand, and sample II, on the other.

The G-test of SOKAL & ROHLF (1987) has been employed for testing null hypothesis of equal abundance of left and right valves of particular bivalve species, which would imply absence of significant post-mortem transportation of bivalve shells. At the significance level of $\alpha=0.05$, the critical value of χ^2 is 3.841. As shown in Table 2, the results do not allow for rejection of the null hypothesis in samples I and III, except for the species *Corbula gibba* and *Ostrea frondosa*.

The two exceptions are hardly surprising, given the differences in size and mechanical resistance of the right and left valves in these two species. In fact, right-valve domination among corbulids is the norm rather than exception (CAUWER 1985). In subsamples IIa and IIb, the sample size of *C. gibba* may be too small to allow for rejection of the null hypothesis. When the two subsamples are combined, the null hypothesis is in fact rejected. Given the evident difference between the right and left valve (*cf.* LEWY & SAMTLEBEN 1979), and given also a constancy in their relative abundance among subsamples (right valves comprise 57—59%), rejection of the null hypothesis for this species cannot be taken as evidence of post-mortem transportation.

In turn, the oyster *O. frondosa* is represented in subsamples IIa and IIb by right valves solely. Given the fact that this species lives with its left valve cemented to the rock, and also the fact that sample II was taken close to the Middle Miocene shoreline (*cf.* RADWAŃSKI 1964), the above observation implies that sample II comes from a mixed fossil assemblage, with *O. frondosa* representing allochthonous elements.

Except *C. gibba*, which has 5—10% of articulated shells, all bivalve species are completely disarticulated (Table 2).

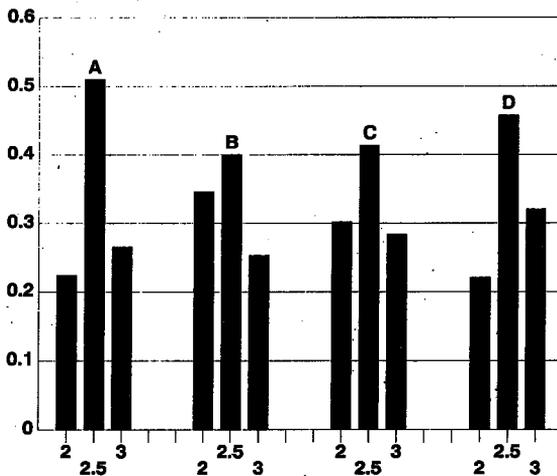


Fig. 5.
Preservation state: sample to sample comparison; detailed explanation in the text
A — Sample I, B — subsample IIa, C — subsample IIb, D — sample III

The proportion of gastropod specimens with their protoconchs preserved is quite substantial, though variable (Table 2). Interestingly, there is little correlation between the proportion of preserved protoconchs and the average preservation state of specimens in any given gastropod species. This absence of correlation implies that processes responsible for protoconch destruction generally different from those causing shell abrasion.

Table 2
Quantitative taphonomic data from the Korytnica Clays

TAXON	SAMPLE	valves:			X ²	α=0.05 n=1 X ² =3.84	TAXON	SAMPLE	shells:			avg. st. pr.
		all	l	r					all	p.	%	
Anadara diluvii	I	52	25	27	0.1	p>0.05	Alvania spp.	IIa	75	34	45.3	2.22
Corbula gibba	I	1856	683	973	51.05	p<0.001	Bittium reticulatum	IIa	82	37	45.1	1.66
	IIa	106	45	61	2.42	p>0.05		IIb	39	16	41	1.59
	IIb	125	58	77	2.68	p>0.05	Nassa hoernesii	I	442	412	93%	2.38
	III	813	330	483	26.97	p<0.001		IIa	41	35	85.2	2.5
C. scalaris	IIa	71	39	32	0.7	p>0.05		III	42	38	90.5	2.42
	IIb	65	31	34	0.14	p>0.05	Natica spp.	I	113	104	92%	2.54
Ostrea frondosa	IIa	76	0	76	-	-		III	42	37	88.1	2.38
Venus multilam.	IIb	75	0	75	-	-	R. auriculata	I	43	28	65.1	2.8
	I	98	50	48	0.04	p>0.05	T. badensis	I	51	29	54.7	1.5

Table 3
Scaphopod fragmentation in the Korytnica Clays

SAMPLE	number of scaphopods:		ratio	confidence interval α=0.05
	shells	fragments		
I	3	19	0.136	0 - 0.279
IIa	1	6	0.143	0 - 0.402
IIb	2	11	0.154	0 - 0.35
III	1	8	0.111	0 - 0.316

Scaphopod shell fragmentation can be described as the ratio of intact shells to the total number of all scaphopod specimens (both shells and shell fragments). As shown in Table 3, this coefficient is fairly constant in the investigated material, though its confidence intervals (calculated according to formula given by REYMENT 1971) are wide.

INDIRECT TAPHONOMIC INFERENCE

Size-frequency distribution (*SFD*) used to be widely analysed in the fossil record (e.g., OLSON 1957; CRAIG & ORTEL 1966; CRAIG 1967; HOFFMAN 1976a, b; BOUCOT 1981; CUMMINS & BAILER 1989), often as an indicator of post-mortem transportation. The *SFD* depends on a number of factors that can hardly be reconstructed in the fossil record. These factors include: growth rate, recruitment type, survivorship curve (for detailed discussion of these variables see CRAIG & ORTEL 1966), predation (HOFFMAN 1976a, b; SHEEHAN & LESPERANCE 1978) and, last but not least, taphonomic processes. Therefore, the only way *SFD* can be employed as a counterargument to the hypothesis of significant post-mortem transportation of fossils is by observation of a variation in *SFD* among species (cf. HOFFMAN 1977) and of a constancy in *SFD* of a species among samples (cf. CUMMINS & BAILER 1989).

As shown in Text-fig. 6, *SFD* is almost identical for *C. gibba* in samples *I* and *III*. In subsamples *Ila* and *Iib*, *SFD* of *C. gibba* is less leptokurtic, thus suggesting that these assemblages represent more time-averaged assemblages (cf. CUMMINS & al. 1986). In turn, *SFD* highly varies among species within any single sample, as exemplified in Text-fig. 6 for sample *I*. Generally, high leptokurtosis and skewness of mollusk *SFD* in all the samples indicate that investigated fossil assemblages are at most weakly time-averaged; for instance, the bimodal *SFD* of *Ringicula auriculata* is suggestive of a non-averaged assemblage produced by instantaneous input of shell material (for discussion see CUMMINS & al. 1986).

TAPHONOMIC PROCESSES — AN INTERPRETATION

The frequency distribution of right versus left valves in bivalve species suggests absence of post-mortem transportation of fossils in the Korytnica Basin. On the other hand, however, the common occurrence of juvenile shells within larger ones is indicative of at least limited local transport. Moreover, total disarticulation of bivalve shells, except for *C. gibba*, may also be taken as an indicator of substantial post-mortem transport.

Four hypotheses can reconcile these observations. First, local transport may not segregate shells larger than 1.5 mm. Second, occurrence of juvenile shells within larger ones may be due to some processes that act in the weathering zone. Third, local transport may have been absent from the areas represented by samples *I* and *III*. Finally, either the test of right-left valve distribution (cf. KORNIČEK & al. 1963), or the test of shell disarticulation (cf. THAYER 1975) fails.

No matter which, if any, of these hypotheses is correct, physical post-mortem transportation of mollusk shells does not seem to have been substantial taphonomic factor in the Korytnica Basin. This conclusion is in fact consistent with actuopaleontological studies on a variety of nearshore environments (e.g., WARME 1969, 1971; PETERSON 1976; BOUCOT 1981).

The significance of biotic transportation can hardly be assessed. Undoubtedly, predatory crabs and fish as well as other predators and scavengers must have transported mollusk shells in the Korytnica Basin. Predatory birds are known to transport and crush large amounts of shells (DRINNAN 1957, WILSON 1967, CARTER 1974). Such activities, however, cannot be reliably deciphered in the fossil record.

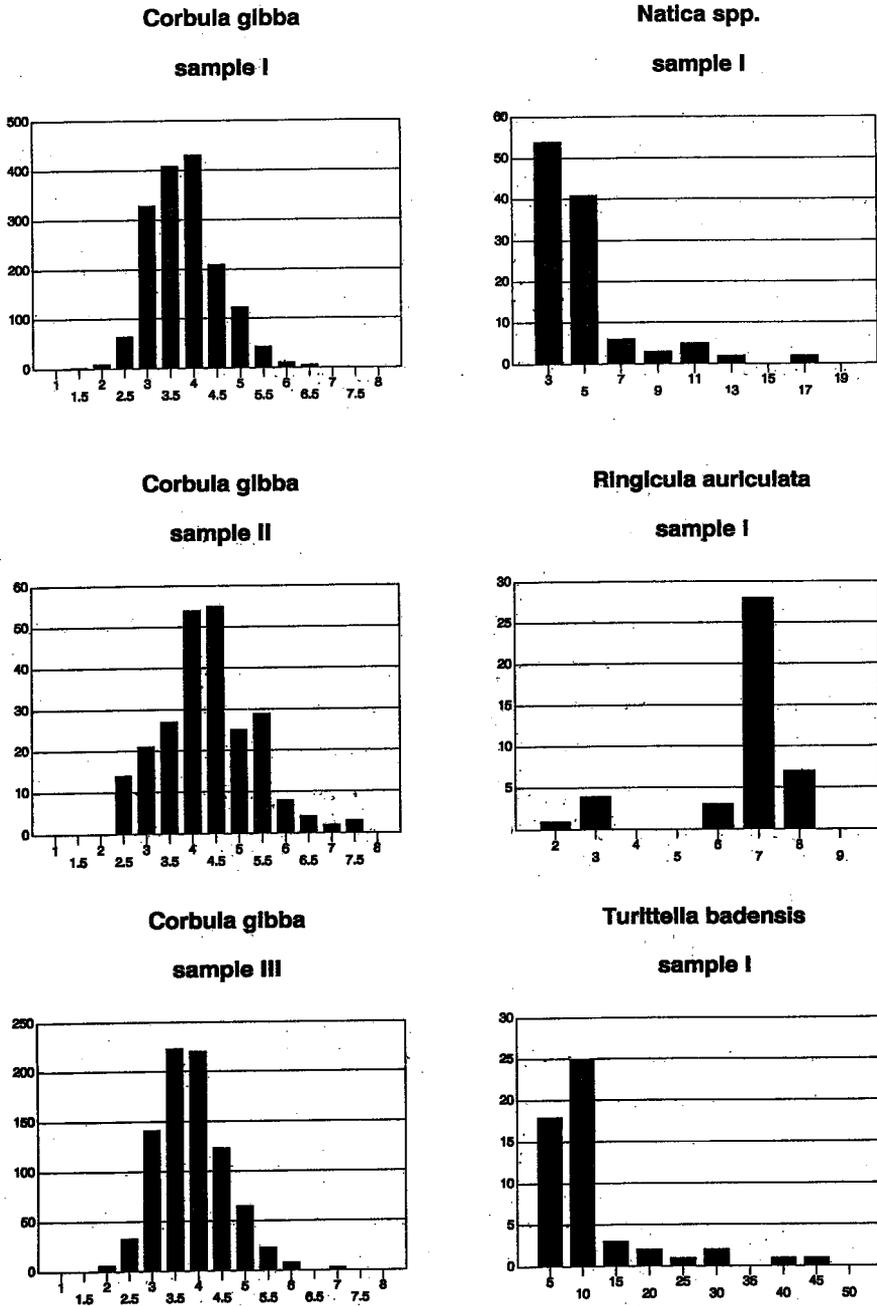


Fig. 6. Indirect taphonomy: Comparison of size-frequency distribution of most abundant species (*Corbula gibba*) among samples, and size-frequency distribution of some abundant gastropods from sample I

FLESSA & BROWN (1983) empirically demonstrated that chemical dissolution processes leave clear evidence on mollusk shells: chalky surface, irregular holes, distal margin thinning, surface etchings. Such features are quite characteristic of some species found in sample *II*, in particular the gastropods *Bittium reticulatum* and *Alvania* spp. When found in samples *I* and *III*, the same species do not show traces of chemical dissolution. In sample *II*, in turn, no other species show traces of chemical dissolution. It seems that the intensity of these chemical processes was too low to affect more resistant species. Alternatively, one might suggest that sample *II* represents a mixed fossil assemblage whose constituents underwent distinctive early taphonomic histories. (It is worth noting that the allochthonous oyster valves also bear evidence of chemical dissolution, thus raising possibility that all shells with such traces come from nearby surf zone).

The scaphopod shell fragmentation seems to be fairly constant among the samples. This observation suggests a dominant role for compaction as the main factor of shell fragmentation, because biotic damage intensity would have vary from one sample to another.

As indicated by analysis of size-frequency distributions of mollusk shells, time-averaging taphonomic processes have more substantially affected sample *II* than the other two samples of the Korytnica Clays. It seems that samples *I* and *III* represent fossil assemblages of a kind close to thanatocoenosis. This conclusion calls for a genetic explanation.

Such an explanation may be provided by the process envisaged by SPEYER & BRETT (1985; see also BEEBE 1989) for the origin of abundant, commonly mono- or oligospecific fossil assemblages found in light-colored, nonstratified mudstones with low to moderate contents of calcium carbonate. The SPEYER & BRETT hypothesis proposes that such assemblages are an effect of very rapid burial by clouds of suspension clay which are storm-generated onshore and transported further offshore. The hypothesis was originally proposed for Paleozoic mudstones containing trilobite clustered assemblages, but the Korytnica Clays may represent an unlithified equivalent of such rocks.

This model is applicable with but a minor modification in the geological context of the Korytnica Basin. Assuming that clouds of suspension clay were storm-generated along the shoreline of the southern slopes of the Holy Cross Mountains, they could have been swept into the Korytnica Basin, or the innermost part of the Korytnica Bay, which acted as a sedimentary trap. An alteration of such events of rapid deposition from suspension clouds with periods of more gradual sedimentation is bound to result in a tapho- thanatocoenotic nature of the fossil assemblage.

Applicability of this model to the Korytnica Clays is supported by a number of arguments. Actupaleontologic observations suggest that the surface layer of sediment at the seabottom (taphonomic active zone, or TAZ) is a zone where intense dissolution processes hinder accumulation of rich assemblages of mollusk shells under the conditions of sustained sedimentation (DAVIES & al. 1989). In fact, the absence of evidence for chemical dissolution, on the one hand, and the commonness of lustrous (even with preserved primary color-pattern) shell surfaces, on the other, suggest a rapid burial of the mollusk fossils (cf. BAŁUK & RADWAŃSKI 1977, POWELL & DAVIES 1989). The Korytnica Basin was at least partly separated from the outer bay (BAŁUK & RADWAŃSKI 1977; but see also SZYMANKO & WÓJCIK 1982, GUTOWSKI 1987) and hence, it could have acted as a sedimentary trap for storm-generated suspension clouds. Finally, gullies (presumably of storm origin) occur in the vicinity of Pińczów, a dozen or so kilometers south of Korytnica, in strata that are time-equivalent of the Korytnica Clays (DREWNIAK 1990).

On the other hand, however, these arguments are weakened by the observations that TAZ may or may not operate at the seabottom (CUTLER 1989; cf. also KIDWELL 1986) and that shell assemblage on Recent beaches in Texas are in fact strongly time-averaged (POWELL & DAVIES 1989). Therefore, the model of burial by storm-generated suspension cloud, although plausible for the Korytnica Clays, must nevertheless be treated with caution.

Assuming this model, however, two distinct taphofacies can be discerned in the investigated material. Samples *I* and *III* (taphofacies *A*) represent thanatocoenoses buried by storm-generated clouds of suspension clay. This implies that all shells within each sample are to be regarded as close

to being isochronous at the ecological timescale, or representative each sample of a single biocoenosis. Subsamples *Ia* and *Ib* (taphofacies *B*), in turn, represent each a somewhat different mixture of cumulative taphocoenosis including poorly preserved specimens and rapidly buried thanatocoenosis including well to perfectly preserved specimens.

Unfortunately, there are at present no criteria to compare the plausibility of this depositional model to the rival model, which assumes that sample *II* represents a mixture of well preserved autochthonous specimens and poorly preserved allochthonous ones. There is, moreover, no way to rule out the possibility that both the models conspired to produce the fossil assemblage of sample *II*. Therefore, the mixed auto- and allochthonous nature of the sample *II* assemblage is herein accepted as a working hypothesis, while the hypothesis of tapho-thanatocoenotic nature of sample *II* is merely regarded as a potential alternative.

CONSTRAINTS IN PALEOECOLOGICAL ANALYSIS

The above presented discussion of taphonomic processes that may have operated in the Korytnica Basin clearly shows a considerable degree of freedom — or even a potential chaos — in taphonomic interpretation. It stems from the lack of an actualistic paradigm that would limit the range of possible inferences. There are a variety of different, but apparently equally plausible, answers to each of the following questions: What are the conditions for formation of time-averaged fossil assemblages? What are the conditions for inactivity of *TAZ*? What is the degree of precision in the methods of detection of post-mortem transportation? Actiopaleontologic researches do not provide unequivocal solutions. Since taphonomic analysis, however, relies, upon actualistic models, a large proportion of its conclusions are necessarily debatable. The present author therefore proposes to restrict the scope of interpretation to those conclusions which either directly follow from paleontologic data, or from unquestionable actiopaleontologic observations. All other interpretations may only have the status of additional working hypotheses and/or educational guesses.

In the case of the Korytnica Clays, the following conclusions can safely be made:

- (i) The state of preservation varies in a consistent manner regardless of the sampling site between species that nominally belong to the same fossilization class (*sensu* LASKER 1976). The high-spined "trouble" gastropod species are an extreme example. Differences in fossilization potential are likely to be the main factor biasing the composition of the fossil mollusk assemblage.
- (ii) Shell fragmentation is fairly constant throughout the basin and most likely reflects effects of compaction.
- (iii) Samples *I* and *III* differ from sample *II* in that time-averaging bias and chemical dissolution processes may be ignored for the former two samples but not for the latter one.
- (iv) The significance of biotic taphonomic factors cannot be estimated.

Given the conclusion (i), relative abundance of species cannot be quantitatively compared among samples, even for species nominally belonging to the same fossilization class and even for fossil assemblages that appear to represent thanatocoenoses. Paleopredation analysis should therefore focus separately on particular species, with interspecific comparisons being made only qualitatively. One may nevertheless assume that a hierarchy of relative abundance of species may sometimes be reliably reconstructed by inference from a number of samples.

Thus paleoecological researches on optimal foraging theory (for review see PYKE & *al.* 1977, HUGHES 1980, PYKE 1984) are generally doomed, though some qualitative conclusions may be reached under favorable conditions.

SHELL-DRILLING GASTROPOD PREDATION

PRE-UNDERSTANDING

HOFFMAN & *al.* (1974) analysed a museum collection in order to discuss the predation by shell-drilling gastropods in the Korytnica Clays. As shown by a comparison of their data to those obtained in the present study (Table 4), significant differences appear for a number of crucial species (*Venus multilamella*, *Corbula gibba*, *Ringicula auriculata*). Hence, the quantitative results provided by HOFFMAN & *al.* (1974; see also HOFFMAN 1976a, b, 1977) can hardly constitute a pre-understanding for the present work.

PREY PALEOECOLOGY

Two prey species only, viz. *Corbula gibba* and *Nassa hoernesii*, are sufficiently abundant in the Korytnica Clays to warrant a discussion in quantitative terms (more than 30 drilled specimens per sample). These two species are discussed below. Additionally, a number of other relatively abundant species are discussed in qualitative terms.

Corbula gibba. Extant corbulid bivalves are marine opportunists, shallow and slow burrowers that inhabit shallow-water muddy to fine sandy substrates and often form dense concentrations, of *Corbula* beds (DAVITASHVILI & MERKLIN 1966, STANLEY 1970, HOFFMAN 1977, LEWY & SAMTLEBEN 1979). They are very commonly attacked by both naticid and muricid gastropods.

Table 4

Comparison of previous data on predation (HOFFMAN & *al.* 1974) with the presently collected material from the Korytnica Clays

TAXON	proportion of drilled specimens			
	HOFFMAN & al. 1974	SAMPLE I	SUBSAMPLES a II b	SAMPLE III
<i>Anadara diluvii</i>	7	8	-	-
<i>Corbula gibba</i>	27	22	25	20
<i>Venus multilamella</i>	6	28	-	-
<i>Bittium reticulatum</i>	19	-	13	-
<i>Nassa hoernesii</i>	10	11	-	12
<i>Ringicula auriculata</i>	2	0	-	-
<i>Turritella badensis</i>	17	15	-	-

Their shells contain, however, a conchiolin layer which enhances both mechanical and chemical resistance of the valve, thus acting as an antipredator device (FISCHER 1963, HOFFMAN & al. 1974, ROBBA & OSTINELLI 1975; but see KARDON 1988).

The species *C. gibba* is the most abundant in each of the three investigated samples of the Korytnica Clays. Nevertheless, it is only in samples *I* and *III* that naticid-drilled specimens of this species occur in number warranting statistical analysis (184 and 69 specimens, respectively); sample *I* contains also 28 muricid-drilled specimens, which number is almost sufficient for sound statistics. Because *C. gibba* has inequivalve shells, for such purposes as the analyses of individual biomass and predator-to-prey size ratio, it has therefore necessary to calculate the size of an absent left valve on the basis of its right companion. To this end, linear regression has been employed (Text-fig. 7), with the correlation coefficient $r = 0.838$ and the following best fit:

$$y = 0.787x + 0.235$$

where y is left and x right valve size.

As indicated by the valve preference test of MATSUKUMA (1980), the null hypothesis of equal frequency of both left and right valve drilling cannot be rejected at the significance level of $\alpha = 0.05$.

As shown in Text-fig. 8, there is no linear correlation between drillhole size and the size of the corbulid prey individual ($r = 0.06$ and 0.02 for naticid drillholes in samples *I* and *III*, respectively; $r = 0.01$ for muricid drillholes in sample *I*). There is no curvilinear correlation either. Since a positive correlation can be expected between predator size and its drillhole diameter (cf. KITCHELL & al. 1981), this result may suggest the absence of predator-to-prey size correlation. The sector-frequency distribution of drillhole location on the valve (Text-fig. 9) indicates that both muricids and naticids preferably attacked the medial part of the valve. This preference is much less pronounced in sample *III* than in sample *I*, but a statistical evaluation (Poisson distribution) is impossible because of the variation in sector area.

The proportion of incomplete drillholes is low (10% in sample *III* at the maximum) and regenerated drillholes are absent. Thus, predation efficiency was quite substantial. Three specimens bear two naticid drillholes each.

The G -test of SOKAL & ROHLF (1987) has been employed to test the null hypothesis that predation intensity was independent of prey size (see Text-fig. 10). The value of G is given by the following formula:

$$G = 2 \sum f_a \cdot \ln (f_a / f_o)$$

where f_a is the number of specimens in a size class, f_o is the expected frequency of the drilled specimens in this size class, provided that drilled specimens occur in equal proportion in all size

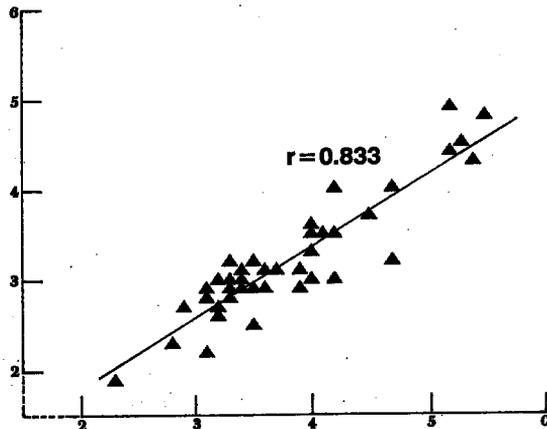


Fig. 7

Valve length to valve width relationship in *Corbula gibba*; r — coefficient of linear regression

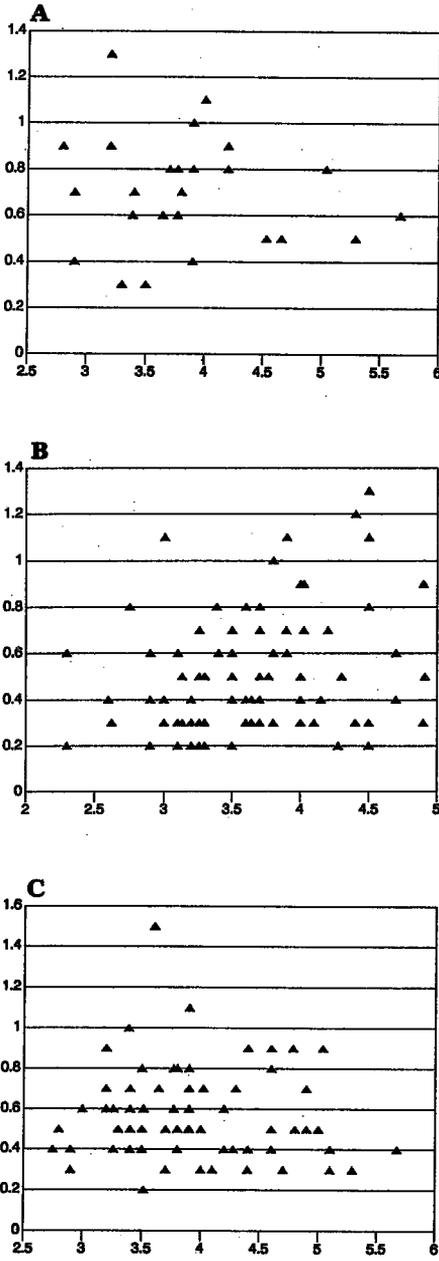


Fig. 8

Relationship of the valve width of drilled individuals of *Corbula gibba* to the drillhole diameter

A — sample I, muricid drillholes; B — sample I, naticid drillholes; C — sample III, naticid drillholes

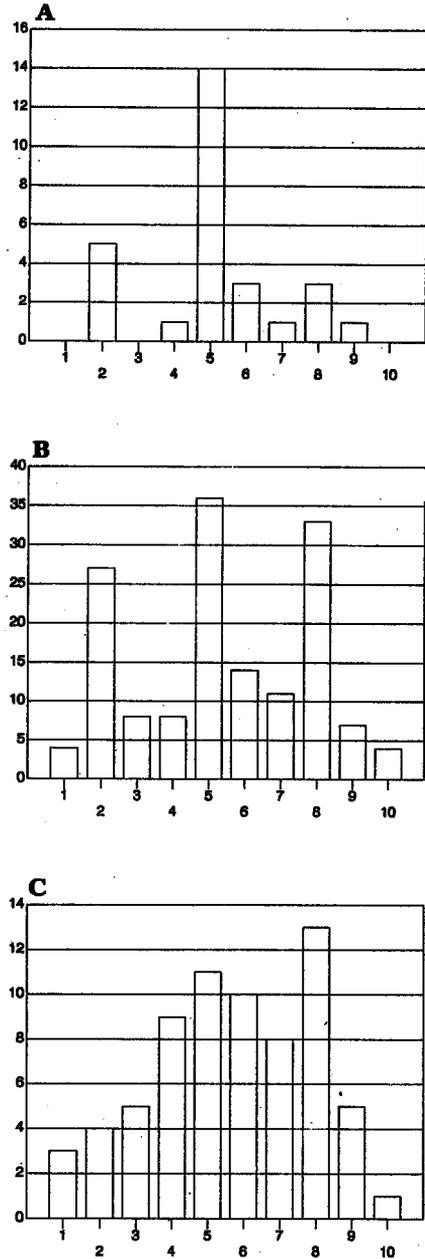


Fig. 9

Sector-frequency distribution of drillholes in valves of *Corbula gibba*

A — sample I, muricid drillholes; B — sample I, naticid drillholes; C — sample III, naticid drillholes

classes. The test does not allow to reject the null hypothesis at the significance level of $\alpha = 0.05$. Shell-drilling predation on corbulid bivalves has been intensely studied in the past (FISHER 1963, TAYLOR 1970, HOFFMAN & *al.* 1974, TAYLOR & *al.* 1983, CAUWER 1985), but the differences in sampling and analytic methods make this results incomparable. CAUWER (1985) observed, however, that the patterns of shell-drilling predation on corbulids do indeed vary. Such a variation occurs also in the Korytnica Clays, as a preference for drillhole location occurs in sample *I* but not in sample *III*, while the proportion of incomplete drillholes is higher in sample *III*. This variation can be best explained by misidentification of naticid versus muricid drillholes (diagnostic hypothesis). Muricid drillholes are more common in sample *I*, hence it is plausible to assume that a larger number of those drillholes have been erroneously assigned to naticid ones; since muricids, however, exhibit a more pronounced preference for drillhole location and are a more efficient predator, misidentification of muricid drillholes for naticid ones could account for the observed effect. It should be noted that the diagnostic hypothesis hinges upon the assumption that sample *I* contains a larger proportion of undoubtedly muricid drillholes, hence it appears a bit tautologic. The alternative ecological hypothesis puts forth that the observed difference between samples *I* and *III* reflects some real ecological or ethological variation in prey-predator relationship. Such a variation is particularly likely given the occurrence of a few naticid species in the Korytnica Clays, whose patterns of spatial distribution are unknown because of their morphological identity at all but the largest sizes.

The species *C. gibba* appears to have been the main prey of naticid gastropods and an important component of the muricid diet (Table 5). This observation, however, may at least partly

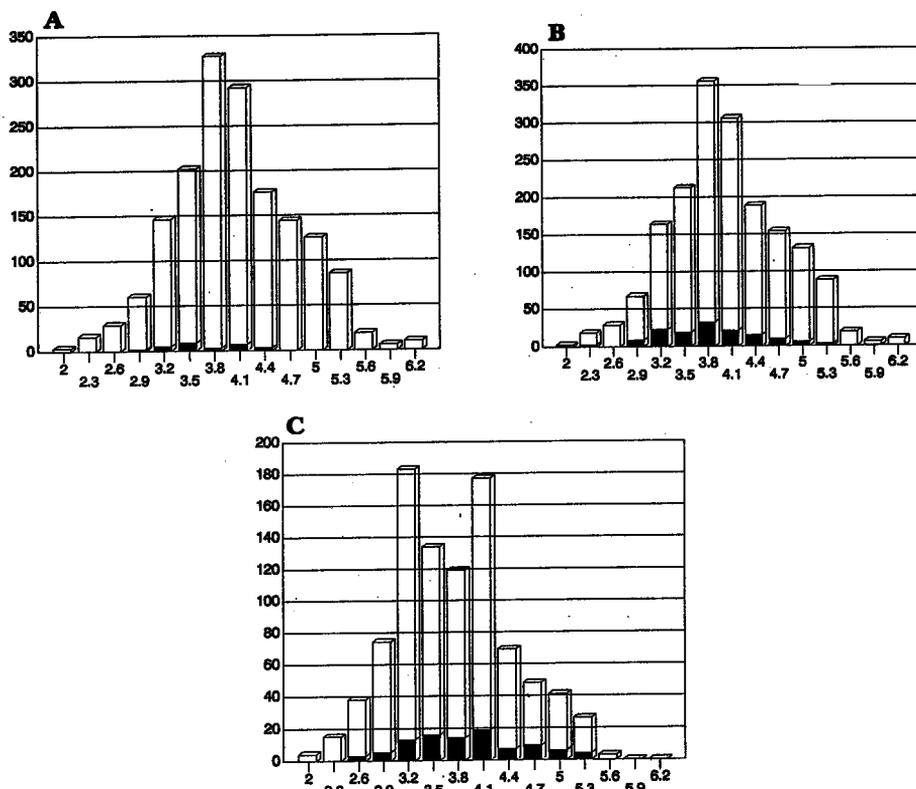


Fig. 10. Size-frequency distribution of drilled (black) and nondrilled (white) valves of *Corbula gibba*

result from some taphonomic bias, provided that the shells of *C. gibba* have had a better chance of fossilization than others. This taphonomic hypothesis can hardly be disproven; although the apparent preference for drillhole location is suggestive of some coadaptation of the shell-drilling gastropods to their corbulid prey and hence, presents a counterargument to the taphonomic hypothesis. The absence of this preference in sample III, where *C. gibba* is most abundant, makes the author to view the latter argument with caution, however.

***Nassa hoernesii*.** Extant nassarid gastropods are highly mobile benthic marine scavengers and predators (DAVITASHVILI & MERKLIN 1968). The species *N. hoernesii* is the most abundant gastropod and the second most abundant mollusk in the three investigated samples of the Korytnica Clays. Nevertheless, it is only in sample I that naticid-drilled specimens of this species occur in numbers warranting a statistical evaluation.

There is no significant linear correlation ($r = 0.62$) between drillhole size and the size of the nassarid prey individual (Text-fig. 11A). There is however, a significant curvilinear correlation ($r^2 = 0.59$), with the following exponential curve providing the best fit:

$$\ln y = 0.14x - 1.16$$

where y is drillhole size and x is prey size. This result differs from the findings concerning *C. gibba* and agrees with expectations of the KITCHELL & *al.* (1981) model.

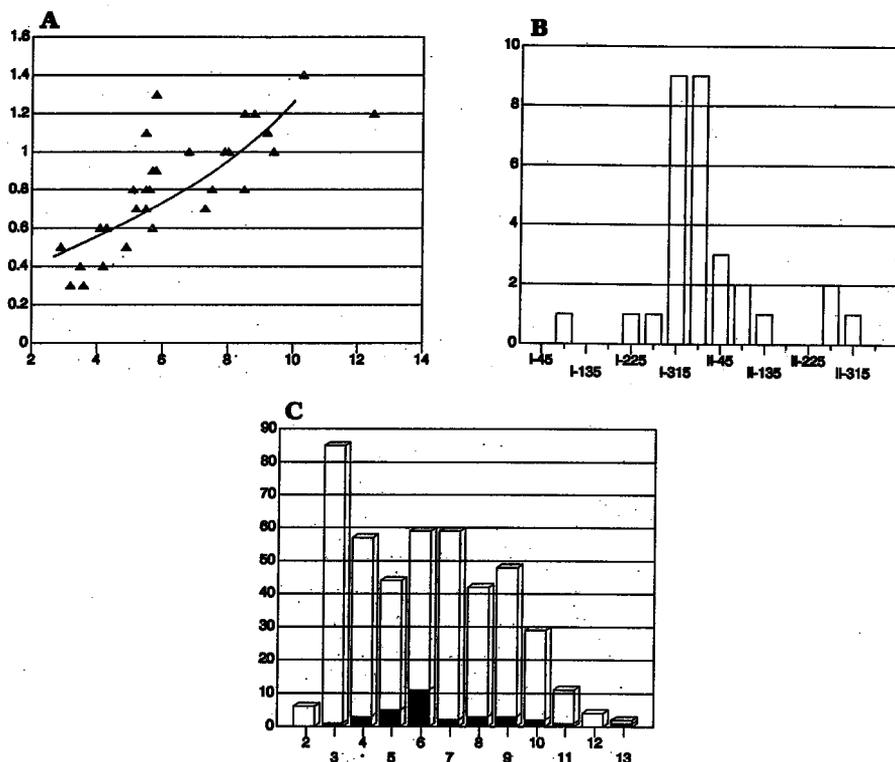


Fig. 11. Naticid predation upon *Nassa hoernesii*, sample I

A — Relationship of shell length to drillhole diameter; B — Sector-frequency distribution; C — Size-frequency distribution of drilled (black) and nondrilled (white) shells

The sector-frequency distribution of drillhole location on the shell (Text-fig. 11B) is indicative of a certain preference, which is emphasized by the occurrence of all drillholes on the two adapertural whorls.

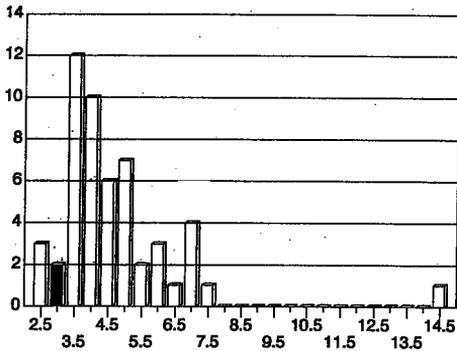
There are no incomplete or regenerated drillholes. Thus, predation efficiency was quite substantial. One specimen bears two naticid drillholes.

The *G*-test of SOKAL & ROHLF (1987) does not allow to reject null hypothesis that predation intensity was independent of prey size (see Text-fig. 11C).

The species *N. hoernes* clearly has been important component of the naticid diet (Table 5), which observation seems to be consistent with the expectation that abundant species should be among the preferred prey.

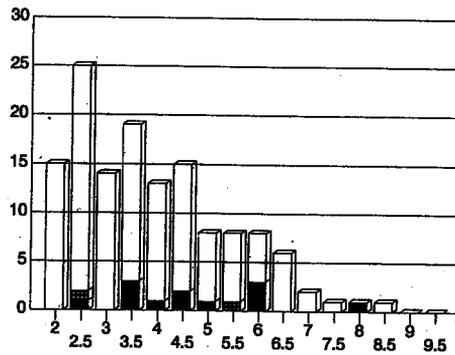
Anadara diluvii

sample I



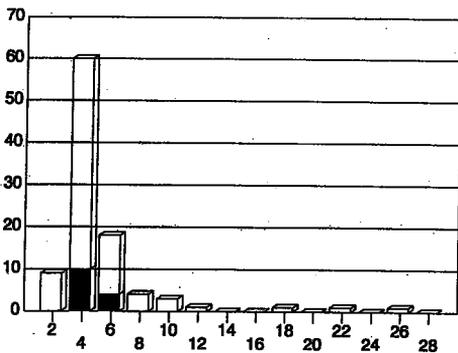
Cyclocardia scalaris

sample I



Venus multilamella

sample I



Natica spp.

sample I

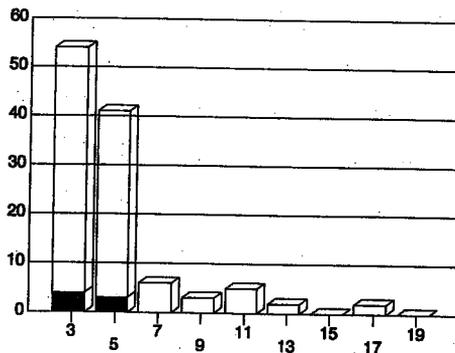


Fig. 12. Size-frequency distributions of drilled (white striped — naticid drillholes; white dotted — muricid drillholes) and nondrilled (white) specimens of selected taxa from the Korytnica Clays

Anadara diluvii. This semi-infaunal bivalve occurs quite abundantly in sample *I* but the only two drilled specimens are juveniles (Text-fig. 12). This result is consistent with observations made previously in the Korytnica Clays (HOFFMAN 1976a) and elsewhere (DUDLEY & DUDLEY 1980). One may suggest that *A. diluvii* adopted the strategy of size-refuge antipredator defence (cf. PAINE 1976).

Cyclocardia scalaris. This epifaunal bivalve occurs quite abundantly in sample *II*. Its shells have been commonly drilled, mostly by naticids and without any preference for a particular size class (Text-fig. 12).

Venus multilamella. This infaunal bivalve occurs commonly in sample *I*. Its juvenile shells have been commonly drilled by naticids (Text-fig. 12), and a size-refuge strategy is strongly suggested.

Alvania spp. These small gastropods occur abundantly in subsample *IIa*, very commonly drilled by muricids. The *Alvania* shells, however, are strongly altered by chemical dissolution and some of the presumed muricid drillholes may in fact be misidentified dissolution perforations.

Bittium reticulatum. This epifaunal gastropod, a "trouble" species, occurs abundantly in sample *II*. Its shells are quite commonly drilled by muricids. As in the case of *Alvania* shells, however, chemical dissolution may substantially bias the observations.

Natica spp. This voracious and mobile infaunal gastropod occurs abundantly in samples *I* and *III*, its juvenile shells bearing evidence of shell-drilling predation (Text-fig. 12). Extant naticids prey on conspecific and even conspecific juveniles, whereas adult specimens are too strong and the energetic cost of preying upon them is too high for other naticids (KITCHELL & al. 1981). Whether or not one deals in the Korytnica Clays with true conspecific cannibalism, cannot be demonstrated, however, since there are more than one naticid species in the fossil assemblage.

Ringicula auriculata. This epifaunal gastropod occurs abundantly in sample *I*, where none of its shell is drilled. This species did fall prey to shell-drilling gastropods, however, as demonstrated by a specimen found in sample *II* as well as by the observations made by HOFFMAN & al. (1974).

Turritella badensis. This semi-infaunal gastropod occurs abundantly in sample *I* and in smaller proportions also in the other samples. A substantial proportion of its shells are drilled, both by naticids and muricids. The *T. badensis* species includes the largest prey specimens found in the Korytnica Clays (more than 28mm in length) as well as the largest drillholes (more than 2mm in diameter).

PREDATOR PALEOECOLOGY

Quantitative data on naticid and muricid predation in the investigated samples of the Korytnica Clays are presented in Table 5. The caveats concerning identification of the shell-drilling predator should be kept in mind, however.

Naticid gastropods

These shell-drilling gastropods feed primarily on infaunal bivalves and gastropods (DAVITASHVILI & MERKLIN 1968, HUGHES 1986; but see REYMENT & al. 1987), mainly in the sublittoral zone though there is even record of extant naticid hunting in the intertidal zone (SAVAZZI & REYMENT 1989).

Two naticid species are abundant in the Korytnica Clays, viz. *Natica millepunctata* and *N. helicina*, and three occur in minor amounts. Juvenile shells of the two dominant naticids are indistinguishable. Hence all observations and conclusions concerning the naticid predation in the Korytnica Clays refer in fact to the genus *Natica* instead of either species.

As evident from Table 5, the Korytnica naticids were highly efficient predators; more than 90% of their drillholes are complete. Completeness of a drillhole does not necessarily demonstrate success of the attack, since some prey species are capable of escape response (CARRIKER

Table 5

Quantitative data on the naticid and muricid predation in the Korytnica Clays

TAXON	No.	Biom.	DRILLHOLES											
			NATICID				MURICIDS							
			s	c	f	d	e	s	c	f	d			
S A M P L E I	<i>Anadara diluvii</i>	26	0.0662	2	2	0	0	0	0	0	0	0	0	0
	<i>Corbula gibba</i>	828	0.9472	156	153	2	1	0	28	28	0	0	0	0
	<i>Cyclocardia scalaris</i>	5	0.0011	0	0	0	0	0	0	0	0	0	0	0
	<i>Venus multilamella</i>	49	0.3439	14	14	0	0	0	0	0	0	0	0	0
	Other species	3	0.0005	0	0	0	0	0	0	0	0	0	0	0
	<i>Alvania</i>	15	0.0105	3	3	0	0	0	1	1	0	0	0	0
	<i>Bittium reticulatum</i>	13	0.0108	1	1	0	0	0	1	1	0	0	0	0
	<i>Nassa hoernesii</i>	443	2.1026	30	29	0	1	0	19	16	1	2	0	0
	<i>Natica</i>	113	1.0172	7	7	0	0	0	0	0	0	0	0	0
	<i>Ringicula auriculata</i>	43	0.2458	0	0	0	0	0	0	0	0	0	0	0
	<i>Turritella badensis</i>	53	0.7422	3	3	0	0	0	5	5	0	0	0	0
Other species	69	0.2478	3	2	0	1	0	6	6	0	0	0	0	
SCAPHOPODA	22	0.0174	0	0	0	0	0	0	0	0	0	0	0	
Σ	1682	5.7532	219	214	2	3	0	60	57	1	2	0	0	
S A M P L E IIa	<i>Anadara diluvii</i>	1	0.0038	0	0	0	0	0	0	0	0	0	0	0
	<i>Corbula gibba</i>	53	0.0819	8	7	0	1	0	2	2	0	0	0	0
	<i>Cyclocardia scalaris</i>	35.5	0.0514	4	4	0	0	0	0	0	0	0	0	0
	<i>Venus multilamella</i>	2.5	0.0782	0	0	0	0	0	0	0	0	0	0	0
	Other species	5.5	0.0007	0	0	0	0	0	0	0	0	0	0	0
	<i>Alvania</i>	75	0.0385	2	2	0	0	0	22	19	1	2	0	0
	<i>Bittium reticulatum</i>	82	0.1010	1	1	0	0	0	10	10	0	0	0	0
	<i>Nassa hoernesii</i>	41	0.2140	8	8	0	0	0	3	3	0	0	0	0
	<i>Natica</i>	25	0.0576	4	4	0	0	0	0	0	0	0	0	0
	<i>Ringicula auriculata</i>	8	0.0441	0	0	0	0	0	0	0	0	0	0	0
	<i>Turritella badensis</i>	25	0.1112	2	2	0	0	0	1	1	0	0	0	0
Other species	39	0.0772	3	3	0	0	0	2	2	0	0	0	0	
SCAPHOPODA	7	0.0069	0	0	0	0	0	0	0	0	0	0	0	
Σ	399.5	0.8665	32	31	0	1	0	40	37	1	2	0	0	
S A M P L E IIb	<i>Anadara diluvii</i>	3.5	0.0258	0	0	0	0	0	0	0	0	0	0	0
	<i>Corbula gibba</i>	67.5	0.1264	5	3	1	0	1	1	1	0	0	0	0
	<i>Cyclocardia scalaris</i>	32.5	0.0565	8	7	1	0	0	1	1	0	0	0	0
	<i>Venus multilamella</i>	1.5	0.0014	0	0	0	0	0	0	0	0	0	0	0
	Other species	6.5	0.0017	1	1	0	0	0	0	0	0	0	0	0
	<i>Alvania</i>	20	0.0111	3	3	0	0	0	5	5	0	0	0	0
	<i>Bittium reticulatum</i>	39	0.0539	0	0	0	0	0	5	5	0	0	0	0
	<i>Nassa hoernesii</i>	22	0.1664	3	3	0	0	0	2	2	0	0	0	0
	<i>Natica</i>	16	0.1768	2	2	0	0	0	0	0	0	0	0	0
	<i>Ringicula auriculata</i>	11	0.0519	1	1	0	0	0	0	0	0	0	0	0
	<i>Turritella badensis</i>	9	0.0745	1	1	0	0	0	2	2	0	0	0	0
Other species	29	0.0561	3	3	0	0	0	2	2	0	0	0	0	
SCAPHOPODA	13	0.0139	0	0	0	0	0	0	0	0	0	0	0	
Σ	270.5	0.8164	27	24	2	0	1	18	18	0	0	0	0	
S A M P L E III	<i>Anadara diluvii</i>	6	0.0229	0	0	0	0	0	0	0	0	0	0	0
	<i>Corbula gibba</i>	406.5	0.4730	69	58	5	0	6	8	6	1	1	0	0
	<i>Venus multilamella</i>	4.5	0.0296	0	0	0	0	0	0	0	0	0	0	0
	Other species	9	0.0282	0	0	0	0	0	0	0	0	0	0	0
	<i>Alvania</i>	2	0.0015	1	1	0	0	0	0	0	0	0	0	0
	<i>Bittium reticulatum</i>	1	0.0008	0	0	0	0	0	0	0	0	0	0	0
	<i>Nassa hoernesii</i>	42	0.1988	5	5	0	0	0	0	0	0	0	0	0
	<i>Natica</i>	42	0.1509	5	5	0	0	0	0	0	0	0	0	0
	<i>Ringicula auriculata</i>	4	0.0232	0	0	0	0	0	0	0	0	0	0	0
	<i>Turritella badensis</i>	9	0.0194	1	1	0	0	0	0	0	0	0	0	0
	Other species	13	0.0325	0	0	0	0	0	0	0	0	0	0	0
SCAPHOPODA	9	0.0110	0	0	0	0	0	0	0	0	0	0	0	
Σ	548	0.9918	81	70	5	0	6	8	6	1	1	0	0	

No. — number of specimens; Biom. — biomass of given species sample population counted after POWELL & STANTON (1985)
 NATICID DRILLINGS: s — all drillholes, c — complete, f — incomplete, d — double,
 e — edge-drillings

MURICID DRILLINGS: s — all drillholes, c — complete, f — incomplete, d — double

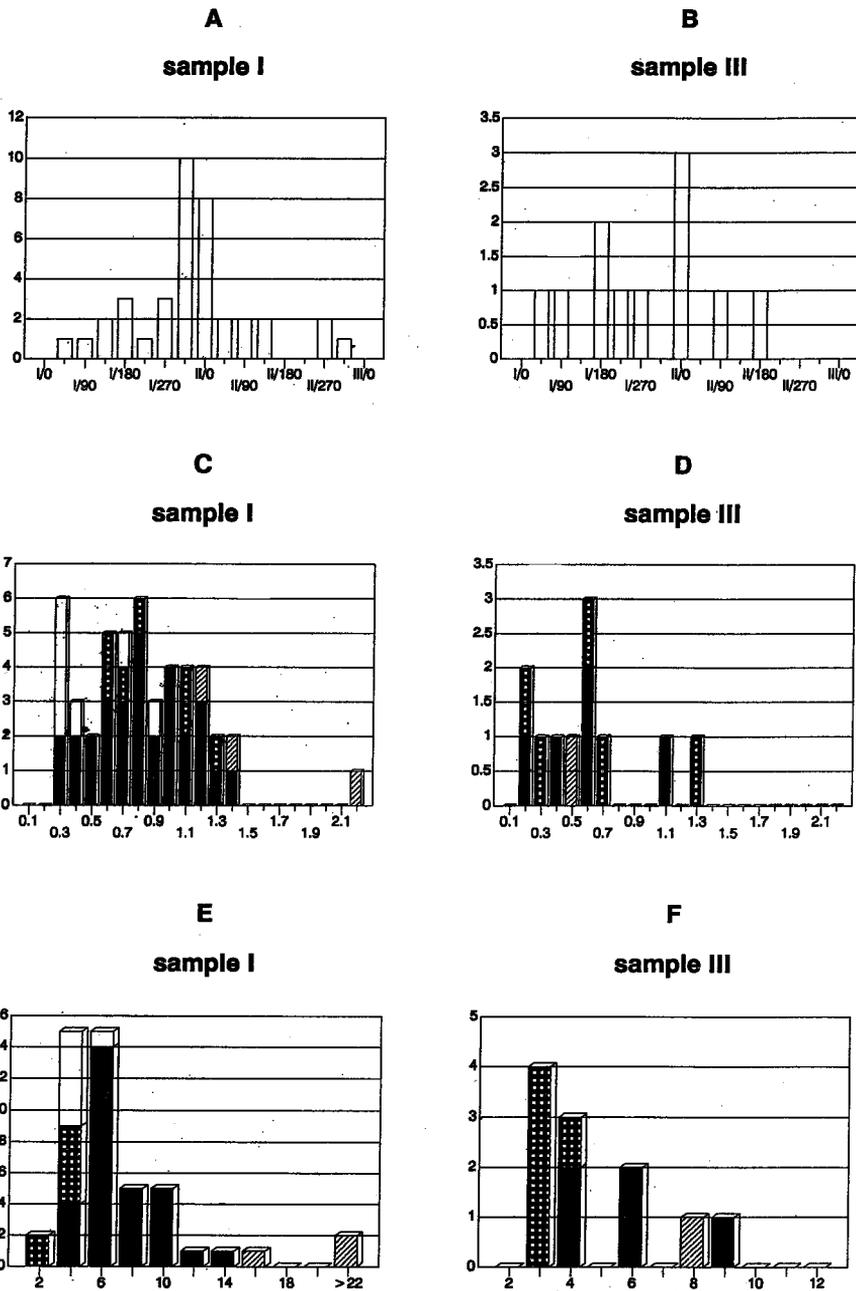


Fig. 13. Naticid predation upon gastropods

A, B — sector-frequency distribution; C, D — size-frequency distribution of drillhole diameter; E, F — size-frequency distribution of drilled shells

Black — *Nassa hoernesii*, White dotted — *Natica* spp., Stripped — *Turritella badensis*, White — Other gastropods

& VAN ZANDT 1972). Such escape response is unlikely to have been an reliable factor in the fossil assemblage of the Korytnica Clays, as there are no regenerated drillholes (for discussion see KITCHELL & *al.* 1986).

In the Korytnica Clays, naticid drillholes are preferably located in the medial part of bivalve shells or in the two adaperatural whorls of gastropod shells. This pattern is more pronounced among small drillholes than among larger ones. More randomness in location of larger drillholes may be due to either weakening of limitation to the prey-handling potential or decreasing behavioral stereotypy with age of the predator (*cf.* BERG 1976).

As shown in Text-fig. 13 the naticid diet also seems to have been changing with age. Juvenile naticids preyed on juvenile *Nassa hoernesii* and a variety of small-sized gastropod species (*Bittium reticulatum*, *Alvania* spp., *Nassa limata*, *Raphitoma plicatella*), whereas adult naticids usually attacked larger-sized *N. hoernesii*, juvenile naticids, and large-sized *Turritella badensis*.

The paleoecological patterns of naticid shell-drilling behavior are remarkably similar in samples I and III. This resemblance is evident in the extreme dominance of *C. gibba* among naticid-drilled mollusks in both samples (Table 5) as well as in comparison of size-frequency distributions of naticid-drilled shells and naticid drillholes (Text-fig. 13) in the two samples. These samples also have a similar taxonomic composition and similar taphonomic characteristics indicative of their thanatocoenotic nature, thus making intersample comparison quite reliable, while their consistency enhances in turn the reliability of paleoecological inference.

Thus, the conditions are unusually favorable for testing the important hypothesis of existence of a specific dietary preference hierarchy among the naticid prey. This hypothesis makes in fact the main premise for all variants of optimal foraging theory, including the KITCHELL & *al.* (1981) model envisaging naticid preferences of prey species according to species-specific cost-benefit ratios.

Two caveats should be made, however. First, it is far from demonstrated that fossilization potential of naticid-drilled specimens is constant among different species. In fact, drillhole presence may in some species more than in others diminish chances of shell preservation, or at least change stratinomic characteristics of the shell (*cf.* LEVER & *al.* 1961, LEVER & THYSSSEN 1968). The high-spined "trouble" species present a particularly acute problem of this sort, since they are most commonly drilled just above the aperture, while adaperatural parts of the shell are only rarely (if ever) preserved in the Korytnica Clays. Significance of these species in the naticid diet is therefore underestimated. Second, there is no way to determine whether the rarity of naticid drillholes in some species (*e.g.*, *Ringicula auriculata*) results merely from the rarity of these species, or whether these species were attacked only exceptionally (due to enhanced vulnerability of particular individuals; *e.g.*, disease) and should actually not be regarded as potential prey (*see* for discussion on limitations mathematical model developed by ESTABROOK & DUNHAM 1976).

Ignoring these caveats, the null hypothesis to be tested is that naticid attack their prey species at random, or that a significant correlation exists between species relative abundance in the fossil assemblage and the number of naticid-drilled individual of a given species. The hypothesis cannot be rejected at the significance level of $\alpha = 0.05$. Obviously, this result is not refutation of the KITCHELL & *al.* (1981) model, but indicates that conditions for its application are not met.

Muricid gastropods

These active epifaunal shell-drilling predators feed primarily on mollusks and barnacles (HOFFMAN & WELDON 1978, BARNETT 1979, PALMER 1982, HUGHES 1986) but also on chitons (HOFFMAN & WELDON 1978); one species is known to live parasitically on shelly mollusks (MATSUKUMA 1977). They prey particularly in the intertidal zone (*e.g.*, WOOD 1968, GARRITY & LEVINS 1981, FAIRWEATHER 1985).

Several muricid species occur in the Korytnica Clays, viz. *Murex friedbergi*, *Ocenebra crassilabiata*, *Ocenebra orientalis*; they are, however, too rare to be found in samples of the size analyzed in the present study. Their foraging activities are nevertheless clearly demonstrated by drillholes, especially in samples I and II (Table 5). In the former sample, muricid drillholes occur in

C. gibba and *N. hoernesii*; in the latter, the most commonly are found in the gastropods *Alvania* spp. and *Bittium reticulatum* which may well be allochthonous elements derived from the nearby rocky shore. As evident from Table 5, the Korytnica muricids were highly efficient predators, though some incomplete muricid drillholes are known from the museum collection (cf. HOFFMAN & al. 1974).

General remarks

Taking the compiled quantitative data (Table 5) on their face value, the muricids hunted much more intensely sample II environment, close to the shoreline, than in more offshore habitats. The Korytnica naticids fed mainly on bivalves, while the muricids preyed largely on gastropods (Text-fig. 14); the findings of some muricid drillholes in *C. gibba* in sample III may in fact reflect misidentification. This division of the feeding niches is emphasized by the fact that the naticids preyed on infaunal and, to a lesser degree, semiinfaunal mollusks, whereas the muricids preyed mostly on the epifauna. It is worth noting, however, that the naticids attacked also gastropods in sample II environment, while the muricids attacked also some shallow-burrowing bivalves in more offshore habitats.

IMPLICATIONS FOR THE QUANTITATIVE PALEOECOLOGICAL ANALYSIS

As noted above, several methodological problems have marred the analysis from the outset. A variation in fossilization potential among mollusk species is perhaps most acute, since it introduces uncertainty about the reconstruction of

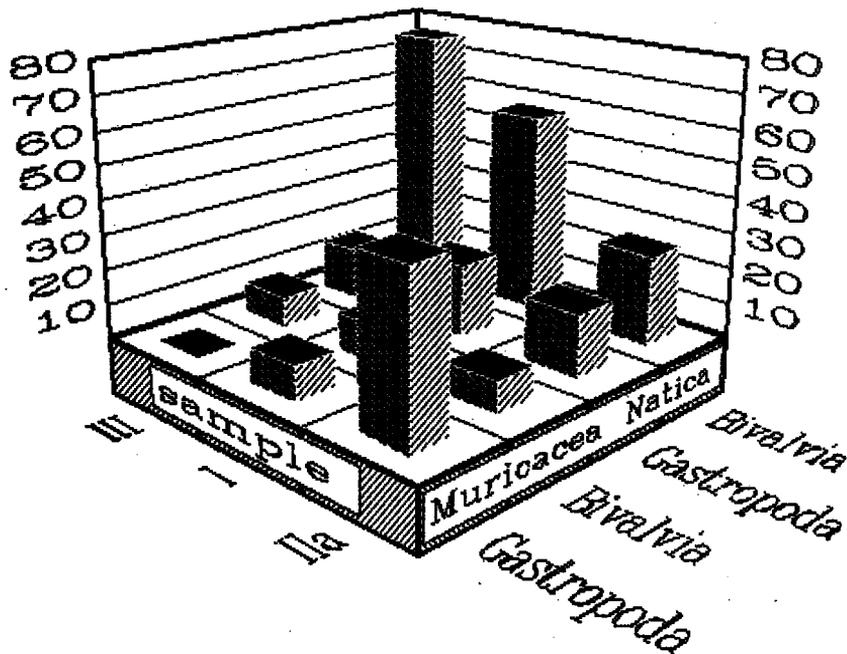


Fig. 14. Data compilation (from Table 5) on muricid and naticid predatory activities in the fossil assemblage of the Korytnica Clays; sum of the bars for each sample is 100%

relative abundance hierarchy of species in sample. Moreover, taphonomic analysis is inconclusive and allows for alternative interpretation. Finally drillhole taxonomy leaves a considerable margin of uncertainty, thus calling for much caution in discussion of the predation patterns.

Consequently, alternative explanations may be offered for a number of the observed quantitative patterns. For example, the confinement of muricid drillholes in sample *III* exclusively to infaunal bivalves (*C. gibba*) can be accounted for by any or all of the following hypotheses:

- (i). Atypical feeding behaviour (ecological hypothesis);
- (ii). Residual nature of the fossil assemblage, with shells of the epifauna having been removed by biostratigraphic processes (taphonomic hypothesis *I*);
- (iii). Smaller fossilization potential of shells of the epifauna (taphonomic hypothesis *II*);
- (iv). Misidentification of naticid drillholes for muricid ones (diagnostic hypothesis).

Listing all these potential explanations decreases subjectivity of the interpretation but does not enhance its reliability.

Paleoecological analysis of the predation by shell-drilling gastropods in the Korytnica Clays must therefore be limited to quite general quantitative patterns (prey-size preference by the predator, drillhole location distribution, predation efficiency) and some qualitative considerations. The conclusions may be regarded as reliable; it should be noted, however, that they do not, and in fact cannot, concern such questions as the impact of shell-drilling predation on population dynamics of the prey, or the preference hierarchy of prey species by the predators, or any quantitative aspect of community ecology. In order to shed true light on these questions, paleoecological data would have to reflect real ecological processes. As indicated by the present hermeneutic analysis of predation paleoecology in the Korytnica Clays, however, this is not the case — either for the Korytnica Clays, or in general. Ecological and paleoecological data are sharply different in nature. The most fundamental difference consists in timescale, since the majority of processes are analysed in function of time. Disciplinary matrix (*sensu* KUHN 1977) of ecology refers to the daily-to-annual timescale, which is beyond the reach of paleoecology. Therefore, all applications of ecological concepts to paleoecology must be treated with a great deal of caution. The first step must always be the question, whether or not a given concept can be soundly extrapolated over a timescale that may inevitably encompass time-averaging of the sample. Quite clearly, such extrapolation is unacceptable for such concepts as, *e.g.*, population dynamics, life-history strategy, energy flow through communities or ecosystems.

One may agree with KITCHELL (1982, 1985b; *see also* KELLEY 1989) that paleontological research on shell-drilling predation shall be more profitable when directed toward more evolutionary questions. Generally “... *our best arguments... will derive from large-scale evolutionary patterns not predicted by existing theories and from data with the potential to discriminate for alternative theories...*” (KITCHELL 1985a, p. 101).

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*Institute of Geology
of the University of Warsaw,
Al. Żwirki i Wigury 93,
02-089 Warszawa, Poland*

Present address:
*Londyńska 15 m. 1,
03-921 Warszawa, Poland*

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M. KOWALEWSKI

ANALIZA HERMENEUTYCZNA DRAPIEŻNICTWA ŚLIMAKÓW DRAŻĄCYCH MIĘCZAKI Z IŁÓW KORYTNICKICH

(Streszczenie)

Przedmiotem pracy jest ilościowa analiza przejawów drapieżnictwa ślimaków drążących wśród mięczaków występujących w iłach korytnickich. Przeprowadzone badania stanowią próbę kontynuacji i weryfikacji analizy dokonanej przez HOFFMANA & al. w 1974 roku (tab. 4).

W związku z historycznym statusem paleoekologii w badaniach zastosowano metodologię hermeneutyczną (fig. 1). Pobrane zostały trzy podwójne próby (fig. 2), których skład taksonomiczny (tab. 1) posłużył do analizy ich reprezentatywności (fig. 4). Kontrola reprezentatywności pozwoliła zaakceptować podpróby prób I i III jako reprezentatywne; podpróby próby II zostały jednak odrzucone i w dalszej części pracy analizowane były niezależnie. Badania paleoekologiczne poprzedzono ilościową analizą tafonomiczną. Rozważono proporcje skorupki małży, stan zachowania muszli i stopień ich fragmentacji, a także rozkład wielkości muszli dla wybranych taksonów. Uzyskane rezultaty (tab. 2—3 oraz fig. 5—6) potwierdzają jakościowe obserwacje badaczy zespołu kopalnego Korytnicy, które wskazują na małe znaczenie procesów tafonomicznych. Liczne podobieństwa (sedymentacyjne, paleoekologiczne i tafonomiczne) zespołu korytnickiego do paleozoicznych zespołów trylobitowych sugerują powstanie zespołu kopalnego Korytnicy na drodze depozycji „zawiesinowych chmur sztormowych”. W świetle tej teorii oraz zgromadzonych danych pobrane próby pochodzą bądź z tanatocenotycznych (próby I i III), bądź tafo-tanatocenotycznych (próba II) zespołów kopalnych.

Ślimaki drążące reprezentowane są przez pięć (w tym: dwa liczne) gatunków należących do rodzaju *Natica* oraz cztery gatunki Muricacea. Ilościową analizę drążeń pod kątem ofiar ograniczono do dwóch najliczniej występujących gatunków: nierównoskorupowego, infaunalnego małża *Corbula gibba* (fig. 7—10) i infaunalnego ślimaka *Nassa hoermesi* (fig. 11). Rozważono preferencje miejsca wiercenia (metodę opisu przedstawiono na fig. 3), skuteczność drapieżnictwa i preferencje wielkości ofiary. Jakościowe wzmianki poświęcono ośmiu taksonom korytnickim (fig. 12). Ślimaki z rodzaju *Natica* atakowały przede wszystkim małża *Corbula gibba* i infaunalne

ślimaki (fig. 13). Drażenia Naticacea liczniej występują w próbach *I* i *III*, pobranych ze strefy sublitoralnej, podczas gdy drażenia Muricacea najliczniej występują w muszlach ślimaków z próby *II*, pobranej z przybrzeżnej facji muszłowca ostrygowego (tab. 5, fig. 14). W świetle zebranych danych nie da się jednak zinterpretować ilościowo złożonych procesów ekologicznych, takich jak: preferencja ofiary przez drapieżcę, wpływ drapieżnictwa na populacje ofiar, czy charakter układu troficznego. Wynika to z ograniczeń narzuconych przez procesy tafonomiczne, zakazy metodologicznego uniformitaryzmu, a przede wszystkim z niemożności operowania paradygmatem ekologicznym w badaniach paleoekologicznych.
