

Nassariid assemblages from the Korytnica Clays – a useful tool for local stratigraphic correlation

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ABSTRACT:

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Analysis of the distribution of species of the family Nassariidae (Gastropoda, Prosobranchia) in the Middle Miocene Korytnica Clays (Holy Cross Mountains, central Poland) enabled five nassariid assemblages to be distinguished, viz. the (1) *Nassarius restitutus*, (2) *N. restitutus-korytnicensis*, (3) *N. korytnicensis*, (4) *N. korytnicensis-limatus* and (5) *Nassarius schoenni* assemblages. The *schoenni* and *korytnicensis-limatus* assemblages occupied the littoral zone of the Korytnica Basin. The remaining nassariid assemblages inhabited different offshore environments. Nassariid assemblages appear to be a useful tool for local stratigraphic correlation as their succession is identical within almost the entire study area, excluding the littoral zone. The lower limit of one of the most widespread nassariid assemblages (*korytnicensis* assemblage) is proved to be an isochronous surface. The isochronous nature of other boundaries between the nassariid assemblages recognised in the succession is also postulated. The entire nassariid sequence is interpreted as a record of temporal changes in the relative size of two large gastropod populations: the population of *Nassarius restitutus* and the population of *Nassarius korytnicensis*. Environmental requirements of the most abundant nassariids are described in detail.

Key words: Nassariidae, Nassariid assemblages, Korytnica Clays, Local stratigraphy, Ecostratigraphy, Middle Miocene.

INTRODUCTION

The Korytnica Clays is a unique facies deposited in the terminal part of a shallow bay that developed in the Miocene along the rocky shore on the southern slopes of the Holy Cross Mountains, central Poland (see RADWAŃSKI 1969; BAŁUK & RADWAŃSKI 1977). These fossiliferous sediments are especially rich in gastropod shells, which represent many different systematic groups (see BAŁUK 1975, 1995, 1997, 2003). The prosobranch family Nassariidae, represented by twenty-five species belonging to four genera is one of the most diversified groups present (see BAŁUK 1997, systematics at generic level based on CERNOHORSKY 1984). Nassariids from the Korytnica Clays not only display a

very high taxonomic diversity but are also the most abundant gastropods in the Korytnica fossil assemblage, as their shells comprise usually more than 40% of all gastropod fossils (see HOFFMAN 1977; KOWALEWSKI 1990).

This paper deals with the distribution pattern of nassariid species in the Korytnica Clays as well as with its palaeoecological and stratigraphic implications. It is focused on the environmental preferences and usefulness of nassariids for local stratigraphic correlation.

Despite the long history of investigation of the Korytnica Clays (see BAŁUK 1984 and HOFFMANN 1987 for a historical review), the distribution pattern of nassariid species within the unit has remained hitherto unrecognised, because most authors focused only on

the taxonomic problems (PUSH 1837; EICHWALD 1853; HÖRNES 1856; FRIEDBERG 1911-1928, 1938; BAŁUK 1997). In the other cases, when nassariids were included in palaeoecological studies, either the sampling was poor and covered only a very small part of the basin (KOWALEWSKI 1990), the nassariids were distinguished at generic level only (HOFFMANN 1977, 1979), or the analysis was exclusively qualitative (BAŁUK & RADWAŃSKI 1977) and imprecise (and undefined) terms, such as “rare” or “common”, were used (KOWALEWSKI 1930).

Calcareous nannoplankton and dinoflagellate cysts locate the Korytnica Clays in the lower part of the Middle Badenian (Upper Langhian to Lower Serravalian – see MARTINI 1977 and GEDL 1996 respectively). A somewhat earlier dating (Lower Badenian, which correlates with the Langhian Stage) was based on benthic foraminifera (RÖGL & BRANDSTÄTTER 1993). In contrast to the well-known stratigraphic position of the

clays, their local stratigraphy (zonation of the clays enabling the correlation of their major exposures) has remained a hitherto unresolved problem. This is because the clays are soft, plastic, and no bedding or any other physical structures can be observed, except for local lamination caused by the shell detritus. Due to the lack of any contrast between the successive portions of the sediment no strictly isochronous surface can be determined. The subdivision of the Korytnica Clays by KOWALEWSKI (1930) and, subsequently, BAŁUK & RADWAŃSKI (1977), is considered here to be unsatisfactory. This is because the subdivision into three members introduced by KOWALEWSKI (1930) is partly incorrect; and that based on three distinct fossil communities, subsequently proposed by BAŁUK & RADWAŃSKI (1977), applies only to some parts of the basin. HOFFMAN’S (1977) investigations would have been definitive, but unfortunately many important fossils were distinguished exclusively at only generic or family level.

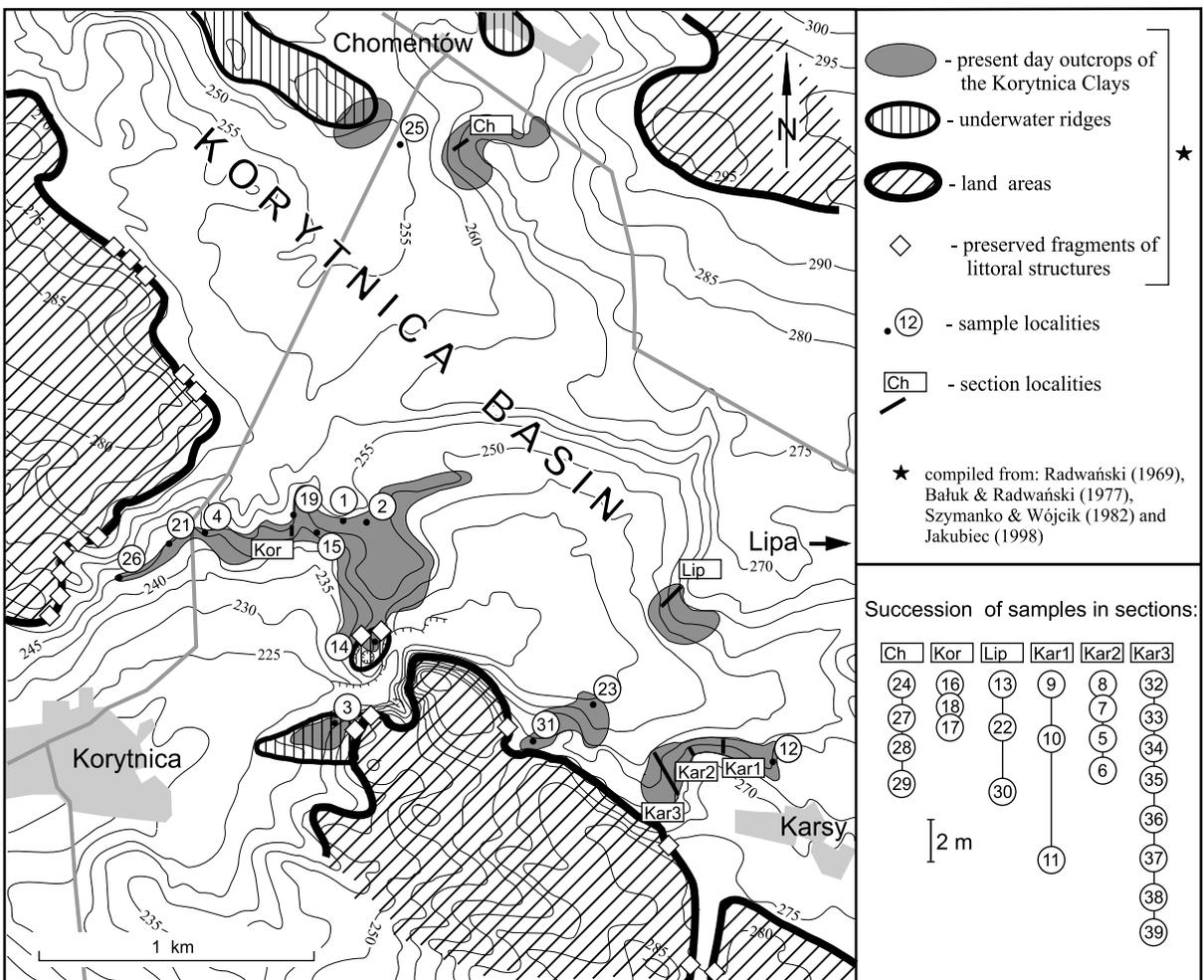


Fig. 1. Palaeoenvironmental sketch of the Korytnica Basin with sample localities

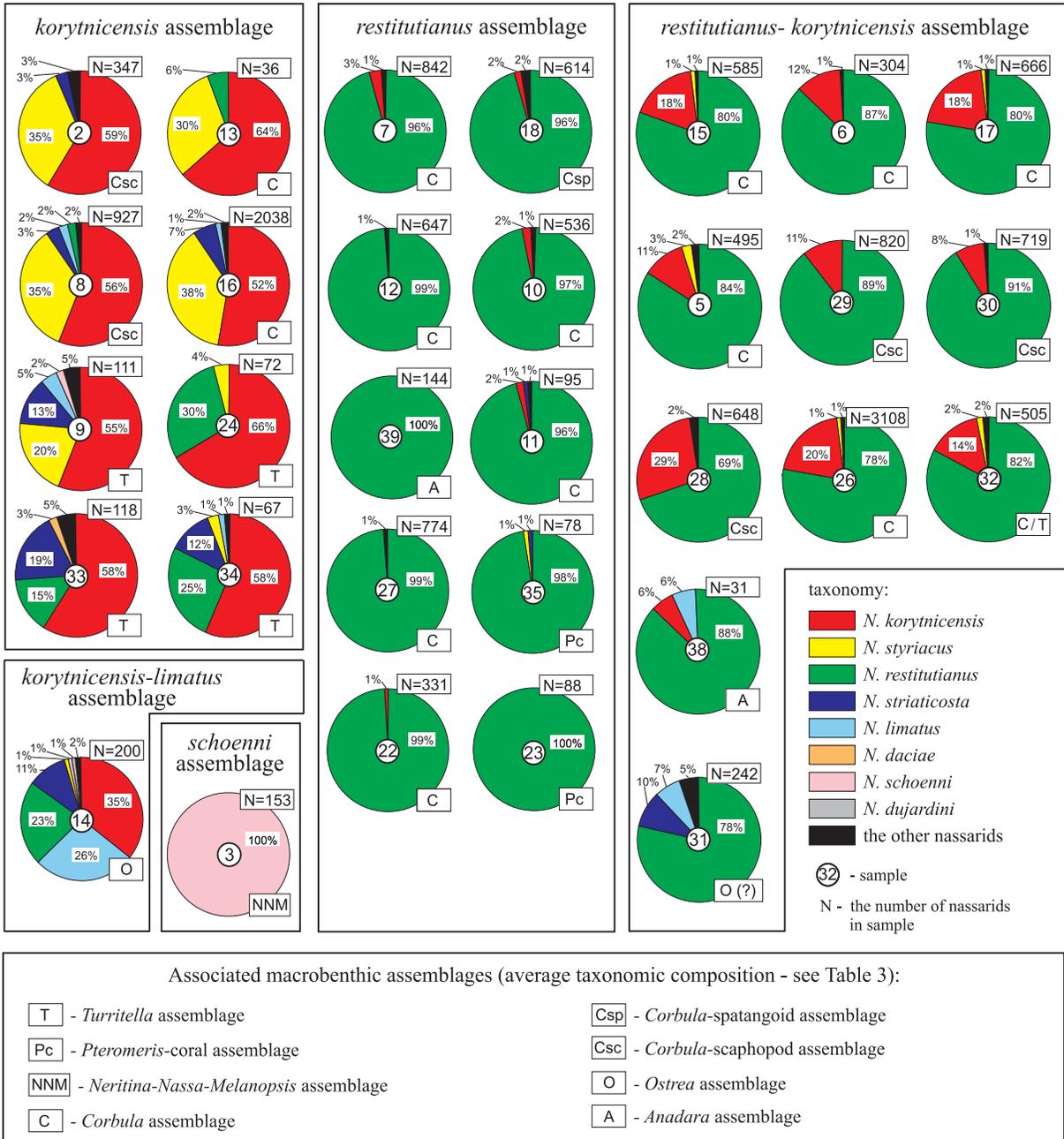


Fig. 2. Nassariid assemblages from the Korytnica Clays and associated macrobenthic assemblages

N. restitutianus-korytnicensis, *N. korytnicensis*, *N. korytnicensis-limatus* and *Nassarius schoenni* assemblages (see Text-fig. 2). Their diagnostic features are summarised in Table 2. The names of the assemblages are derived from the most abundant species.

In most cases, the nassariid taxonomic composition of each assemblage is distinct. The only exceptions are the *N. restitutianus* and *restitutianus-korytnicensis* assemblages, which seem to be fairly similar. However, despite this similarity, they are distinguished by the rel-

ative abundance in each of the dominant taxon, *Nassarius restitutianus* (see Text-fig. 4).

The relative frequencies of nassariid species recognised in most of the samples probably reflect differences in the original communities. This is because the Korytnica fossil assemblage is at most only weakly time-averaged and the remains of organisms from the Korytnica Clays underwent no, or only slight, post-mortem transportation or dissolution (KOWALEWSKI 1990, KOWALEWSKI & MIŚNIAKIEWICZ 1993).

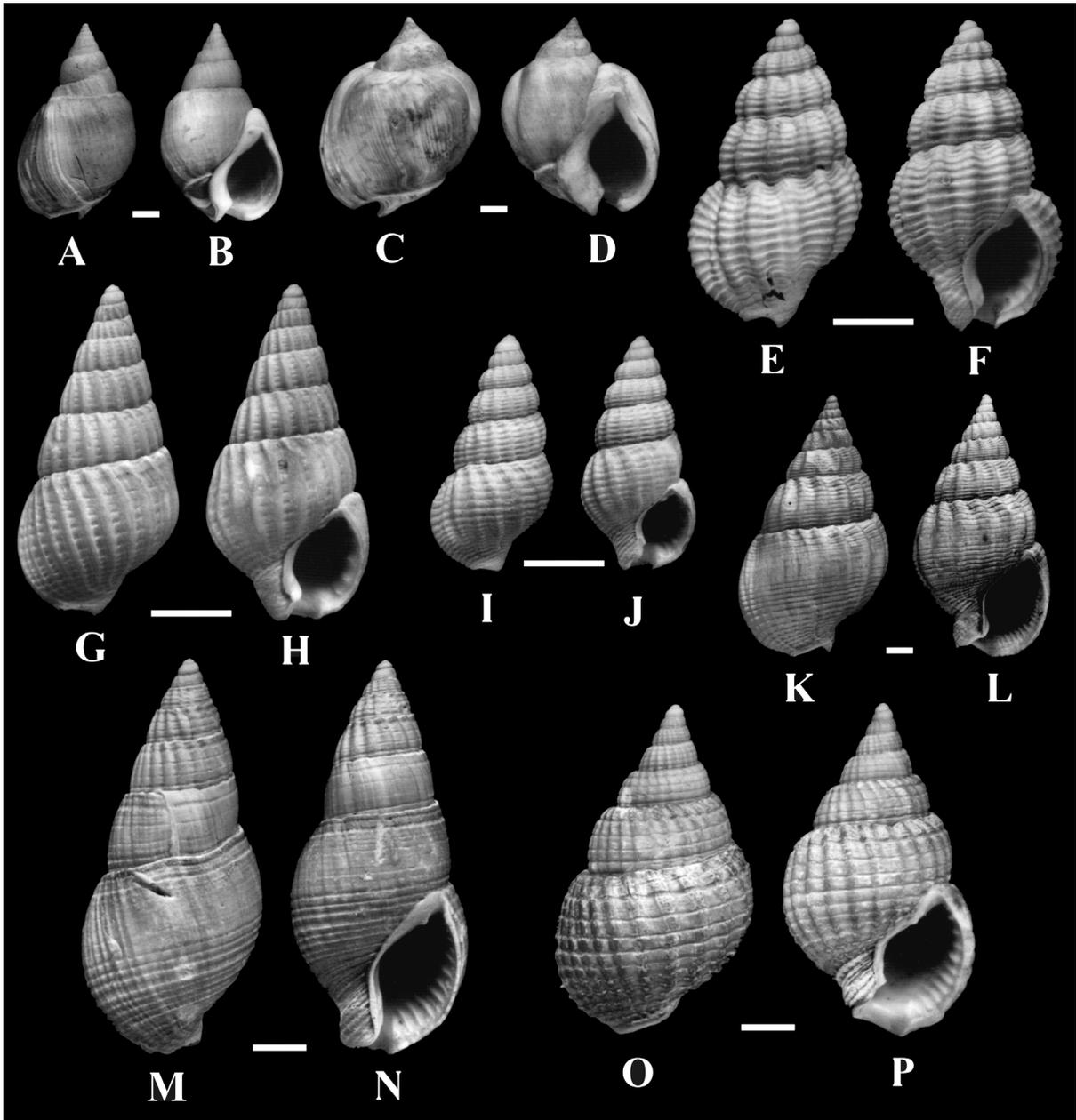


Fig. 3. Most common nassariids from the Korytnica Clays. A, B. *Nassarius dujardini* (DESHAYES, 1844). Shell MWG/ZI/32/010 in abapertural and apertural views. C, D. *Nassarius schoeni* (HOERNES & AUINGER, 1882). Shell MWG/ZI/32/011 in abapertural and apertural views. E, F. *Nassarius daciae* (HOERNES & AUINGER, 1882). Shell MWG/ZI/32/012 in abapertural and apertural views. G, H. *Nassarius styriacus* (AUINGER in HILBER, 1879). Shell MWG/ZI/32/013 in abapertural and apertural views. I, J. *Nassarius striaticosta* (BOETTGER, 1906). Shell MWG/ZI/32/014 in abapertural and apertural views. K, L. *Nassarius limatus* (CHEMNITZ, 1786). Shell MWG/ZI/32/015 in abapertural and apertural views. M, N. *Nassarius restitutus* (FONTANNES, 1879). Shell MWG/ZI/32/016 in abapertural and apertural views. O, P. *Nassarius korytnicensis* (BALUK, 1997). Shell MWG/ZI/32/017 in abapertural and apertural views. Scale bars = 0.2 cm. Specimens are housed at the Faculty of Geology, Warsaw University, Poland (abbreviated MWG). All photos taken by B. MALINOWSKA

Additionally, the results of actuo-palaeontological studies clearly show that the fossilisation potential is generally similar within the entire gastropod group (PETERSON 1976; FLESSA & BROWN 1983). The relative frequencies of the gastropods observed in clays deposited on the

slopes of the Łysa Mountain (sample 14) would be the only possible exception to this, because in this locality the counteracting effects of time-averaging enrichment vs. taphonomic loss strongly biased the original ecological information (see KOWALEWSKI & MIŚNIAKIEWICZ 1993).

nassariid assemblages	relative frequency of nassariid species [%]									samples
	<i>Nassarius restitutianus</i>	<i>Nassarius korytnicensis</i>	<i>Nassarius limatus</i>	<i>Nassarius styriacus</i>	<i>Nassarius striaticosta</i>	<i>Nassarius daciae</i>	<i>Nassarius schoenni</i>	<i>Nassarius dujardini</i>	the other nassariids	
<i>restitutianus</i> assemblage	≥ 96	≤ 3	< 1	≤ 1	≤ 1	< 1	< 1	0	< 1	7, 10, 11, 12, 18, 22, 23, 27, 35, 39.
<i>restitutianus-korytnicensis</i> assemblage	70-90	≤ 29	≤ 7	≤ 3	≤ 10	< 1	< 1	0	< 1	5, 6, 15, 17, 26, 28, 29, 30, 31, 32, 38.
<i>korytnicensis</i> assemblage	≤ 30	50-66	≤ 5	≤ 38	≤ 19	≤ 3	≤ 2	< 1	< 1	2, 8, 9, 13, 16, 24, 33, 34.
<i>korytnicensis-limatus</i> assemblage	23	36	25	1	11	0	1	1	1	14
<i>schoenni</i> assemblage	0	0	0	0	0	0	100	0	0	3

Table 2. Diagnostic features of nassariid assemblages from the Korytnica Clays

Areal distribution of nassariid assemblages The *korytnicensis* assemblage occurs throughout the entire Korytnica Basin. Samples characterised by a relatively high frequency of *Nassarius styriacus* are located in the central part of the basin. The latter species is replaced northwards by *Nassarius restitutianus* and southwards by *N. restitutianus* and *Nassarius striaticosta* (Text-fig. 5A).

The *restitutianus* and *restitutianus-korytnicensis* assemblages also occur throughout the entire Korytnica Basin area (Text-fig. 5B, C). A relatively high frequency of *N. limatus* is observed in samples taken from the southern part of the basin. The unique sample (31), which is characterised by the relative frequency of *N. restitutianus* typical of the *restitutianus-korytnicensis*

assemblage but lacks *Nassarius korytnicensis*, was also encountered there (Text-fig. 5C).

The *korytnicensis-limatus* and *schoenni* assemblages occur in the southern marginal part of the basin (Text-fig. 5D), near to the Miocene underwater ridges postulated by BAŁUK & RADWAŃSKI (1977).

Stratigraphic distribution of the nassariid assemblages

The succession of nassariid assemblages in particular parts of the Korytnica Basin is shown in Text-fig. 6. The most complete sequence was recognised in the Kar3 section. From bottom upwards there appear successively: the *restitutianus*, *restitutianus-korytnicensis*, *restitutianus*, *korytnicensis* and *restitutianus-korytnicensis* assemblages. Due to the extremely low number of nassariid shells in samples 36 and 37 it is impossible to determine precisely which nassariid assemblage(s) occurs in the lower part of the section, between the first appearance of the *restitutianus-korytnicensis* assemblage and the second appearance of the *restitutianus* assemblage. It can only be inferred that the nassariid community represented by sample 36 was dominated by *N. restitutianus* because all the few nassariid shells found represent this species.

The Chomentow (Ch), Korynica (Kor), Lipa (Lip), and Karsy 2 (Kar2) sections (see Text-fig. 1 and 6) are characterised by the occurrence of an identical sequence of nassariid assemblages, i.e. the *restitutianus-korytnicensis*, *restitutianus*, and *korytnicensis* assemblages. The same sequence, represented by samples 38, 35, 34 and 33, was also recognised within the Kar3 section discussed above.

The relative position of the particular nassariid assemblages observed within the Kar1 section also agrees with the succession reported from the Kar3 locality.

A brief comparison of the sequences recognised within the particular sections clearly shows that the suc-

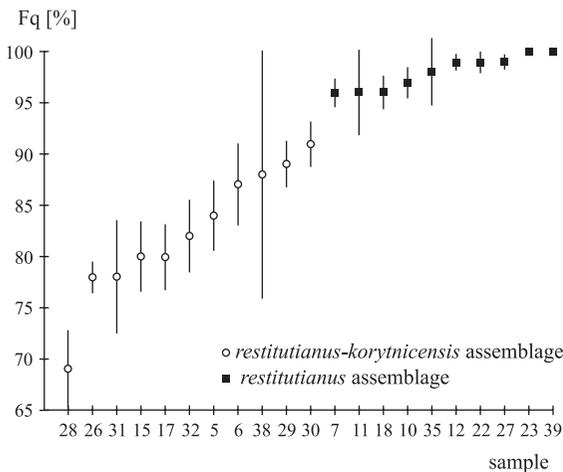


Fig. 4. Relative frequency of *Nassarius restitutianus* (Fq) in individual samples representing the *restitutianus* and *restitutianus-korytnicensis* assemblages. Note the much more dispersed distribution of Fq in the *restitutianus-korytnicensis* assemblage and the gap between sample 30 and sample 7. Confidence intervals computed from the formula $p \pm 1,96 \sqrt{\frac{p(1-p)}{n}}$, where p denotes the proportion of one kind of fossil observed in a sample of n specimens (ŁOMNICKI 1995)

cession of nassariid assemblages was the same throughout the study area. The complete sequence apparently consists of the *restitianus*, *restitianus-korytnicensis*,

restitianus, *korytnicensis* and *restitianus-korytnicensis* assemblages, all of which were recorded only in the Kar3 section.

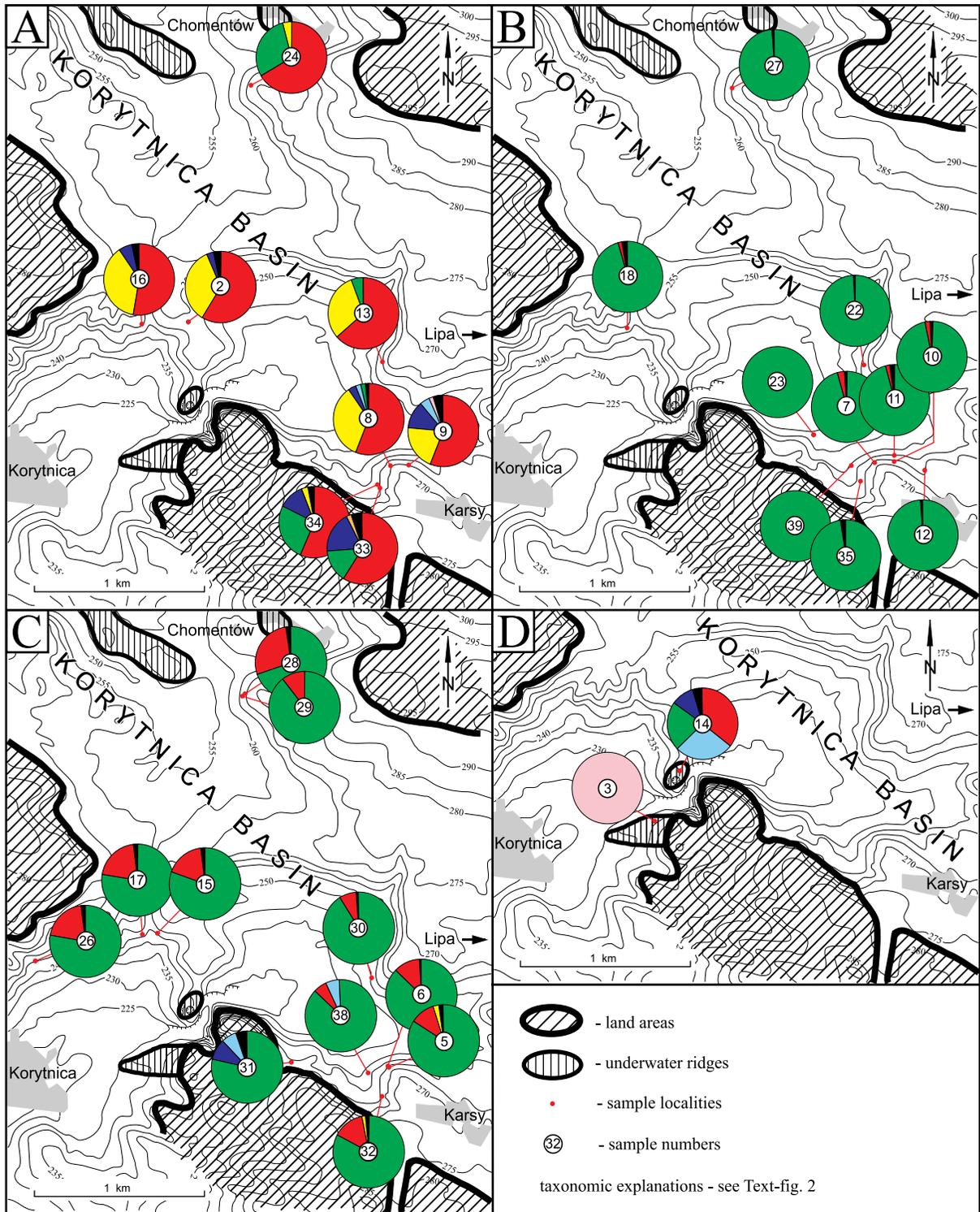


Fig. 5. Areal distribution of nassariid assemblages in the Korytnica Basin

Accompanying fauna HOFFMAN (1977) distinguished and interpreted eight fossil macrobenthic assemblages from the Korytnica Clays (see Table 3).

Most of them were also recognised within the investigated material (see Text-fig. 2). One new fossil assemblage was recognised in the present study. It is repre-

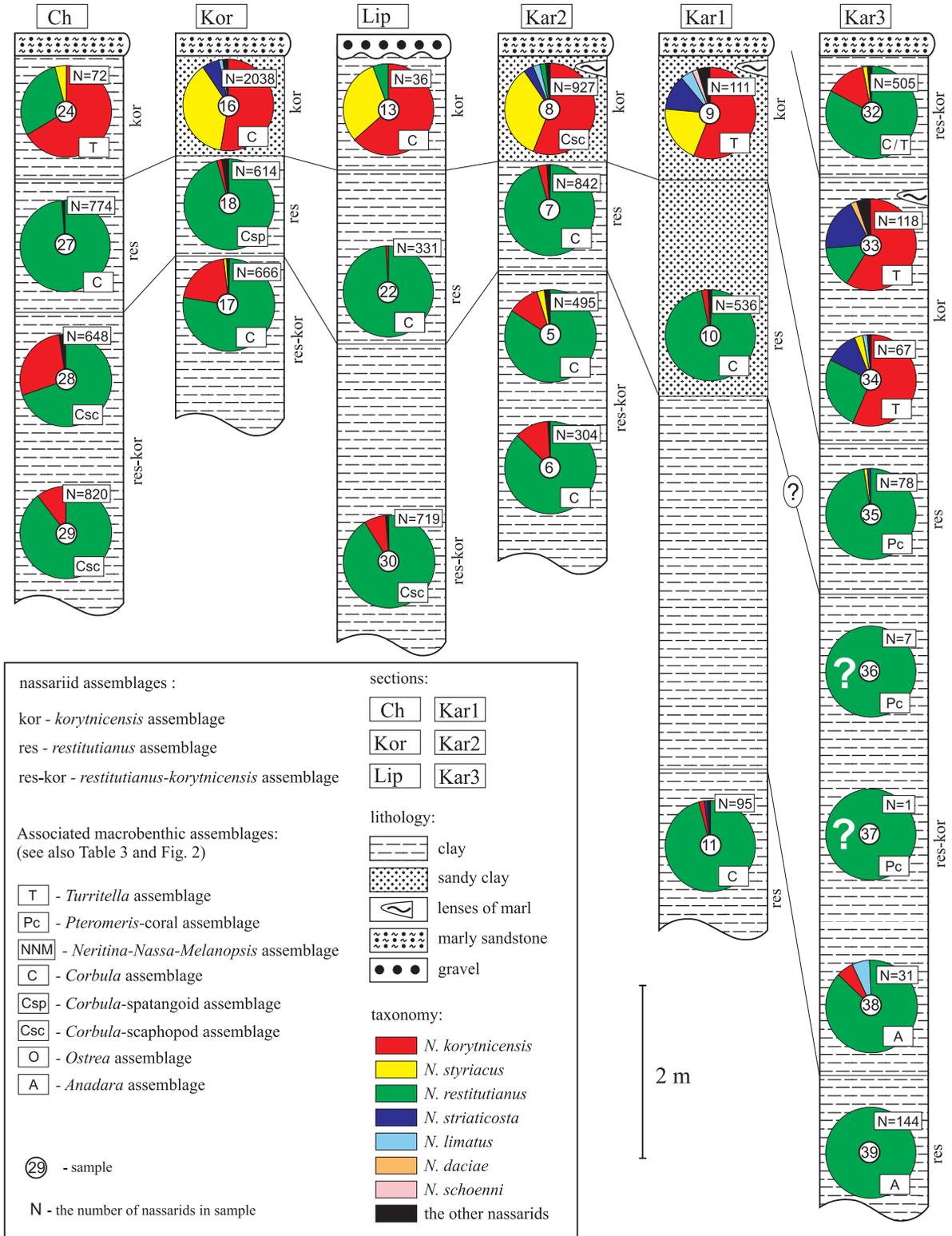


Fig. 6. Stratigraphic distribution of the nassariid assemblages and associated macrobenthic assemblages in the Korytnica Basin

macrobenthic assemblage	average relative frequency of basic taxa	palaeoenvironmental interpretation
<i>Ostrea</i> assemblage *	<i>Ostrea</i> (30%) bryozoans (20%) <i>Petalococonchus intortus</i> (12%)	Unprotected onshore environment characterised by very clear and turbulent water. Bottom deposit with large amounts of sand-size and gravel size particles.
<i>Neritina-Nassa-Melanopsis</i> assemblage *	<i>Ostrea</i> (20%) <i>Neritina picta</i> (40%) <i>Nassarius schoeni</i> (20%) <i>Melanopsis</i> (11%)	# Poorly oxygenated coastal swamps.
<i>Turritella</i> assemblage *	<i>Turritella</i> (40%) <i>Corbula gibba</i> (12%) <i>Odostomia</i> (10%)	Marginal shallow muddy flats characterised by soft and fluid bottom and relatively clear water. Marine plants absent, bottom deposit rather poor in organic matter. High-energy environment.
<i>Corbula</i> assemblage *	<i>Corbula gibba</i> (80%)	Very high water turbidity. Marine plants absent, bottom relief rather stable and bottom sediment rather poor in organic matter.
<i>Corbula</i> -spatangoid assemblage *	<i>Corbula gibba</i> (40%) <i>Turritella</i> (12%) numerous echinoid (spatangoid) tests	Soft bottoms of very sheltered sites characterised by rather poor water circulation. Water rather turbid and bottom sediment rather poor in organic matter. Seagrass absent but sediment surface partly covered by some algae.
<i>Corbula</i> -scaphopod assemblage *	<i>Corbula gibba</i> (50%) <i>Fustiaria</i> (10%) naticids (8%)	Fairly quiet and clear-water areas. Bottom relief rather stable without seagrass cover.
<i>Turboella-Loripes</i> assemblage *	<i>Turboella</i> (20%) <i>Loripes</i> (15%) cerithids (12%) <i>Corbula gibba</i> (10%)	Fairly quiet and clear-water areas. Bottom relief rather stable with a more or less dense seagrass cover.
<i>Pteromeris</i> -coral assemblage *	<i>Pteromeris</i> (30%) <i>Corbula gibba</i> (8%) numerous solitary corals	Rather clear- and quiet-water environment, with low sedimentation rate. Marine plants generally absent. Some benthic algae occurring in minor proportions. Bottom deposit rather firm and relatively poor in organic matter.
<i>Anadara</i> assemblage (x)	<i>Anadara diluvii</i> (33%) nassarids (18%) <i>Corbula gibba</i> (12%) <i>Turritella badensis</i> (6%) numerous echinoid (spatangoid) tests	Relatively high sedimentation rate, bottom covered by macroalgae.

Table 3. Macrobenthic assemblages recognised hitherto from the Korytnica clays: * – recognised and interpreted by HOFFMAN (1977), (x) – recognised and interpreted during this study, # – this interpretation appears for the first time in BALUK & RADWAŃSKI (1977)

sented by samples 38 and 39 and, due to the relatively high frequency of the bivalve mollusc *Anadara diluvii* (30-35% of all invertebrate fossils), it is referred to here as the *Anadara* assemblage. The remaining components of this assemblage comprise nassarids (11-25%), *Corbula gibba* (10-14%), *Turritella badensis* (5-10%), *Natica tigrina* (4-9%), numerous echinoid tests and small numbers of *Apporhais*.

Among the assemblages recognised from the Korytnica Clays, the most abundant are those characterised by the relatively high frequency of *C. gibba* (the *Corbula*, *Corbula*-spatangoid and *Corbula*-scaphopod assemblages). A significant proportion of *C. gibba* in the investigated material indicates a low sedimentation rate, because this small bivalve mollusc is a sluggish, shallow burrower unable to escape after a burial event (YONGE 1946). In Recent communities characterised by such a high frequency of corbulids as is observed in the

Corbula assemblage, the sedimentation rate is in fact extremely low (LEVY & SAMTLEBEN 1979). Because of the occurrence of solitary corals a low sedimentation rate was also postulated for the *Pteromeris*-coral assemblage (see Table 3).

Unlike the assemblages discussed above, the newly recognised *Anadara* assemblage is characterised by the absence of corals, and a relatively low frequency of *C. gibba*. Recent representatives of *Anadara* belong to the mobile semi-infauna (ABBOTT 1968). *Anadara diluvii*, lacking both a byssal gap and pallial sinus, probably displayed a similar mode of life. The absence of corals and the domination of the vagile semi-infaunal arcid over the sluggish corbulid burrower suggest a relatively high sedimentation rate for the *Anadara* assemblage. The occurrence of *Apporhais* indicates the presence of algae, as recent species of this genus feed on decaying macroalgal remains (BARNES & BAGENAL 1952).

The *Ostrea* assemblage was recognised formerly from the clays on the slopes of Łysa Mountain (sample 14 herein) (see RADWAŃSKI 1969; HOFFMAN 1977). This assemblage, recognised herein also in sample 31, differs from the typical one in respect of the lower frequency of oyster shells and littoral bryozoans. Apart from that, the sample is characterised by the great abundance of the foraminifer genus *Amphistegina*, usually considered as indicative of seagrass vegetation (see RADWAŃSKI 1969 and references therein). Sample 31 thus probably represents a deeper littoral environment, or one intermediate between a littoral and a shallow-water environment, characterised by the occurrence of marine plants.

The assemblage of sample 32 is intermediate between the *Corbula* assemblage and the *Turritella* assemblages. Because of this, invertebrate remains from the sample are considered here to be indicative of a slightly deeper and less energetic environment than the environment of the *Turritella* assemblage (see Table 3).

LOCAL STRATIGRAPHY OF THE KORYTNICA CLAYS

Previous investigations KOWALEWSKI (1930) distinguished three members within the Korytnica Clays: (1) the oyster shell-bed lying directly on Jurassic substrata, considered to be the lowermost one, (2) the middle one with many different molluscs and (3) the uppermost member characterised by the enormous diversity of the mollusc fauna. Subsequent investigations mostly refuted this subdivision. FRIEDBERG (1931), RADWAŃSKI (1969) and BAŁUK & RADWAŃSKI (1977) proved that the oyster shell-bed was only a littoral facies of the Korytnica Clays. Also questionable is the detailed taxonomic description of the middle member. According to KOWALEWSKI (1930; p. 18), the middle part of the Korytnica Clays does not contain *Fustiaria jani*. However, a few pages later the same author stated that *F. jani* did occur in that part of the clays (KOWALEWSKI 1930; p. 163). The upper member, which contains a high-diversity mollusc assemblage, seem to be the only one of KOWALEWSKI's (1930) units with practical potential (cf. BAŁUK & RADWAŃSKI 1977).

The fossil assemblage of KOWALEWSKI's (1930) upper member seems to correspond to community III of BAŁUK and RADWAŃSKI's (1977) three-fold subdivision of the Korytnica Clays. The following organic communities were recognised within these units: (i) Community I, characterised by the solitary coral *Flabellum*, the scaphopod *Dentalium badense* and gastropod *Turritella*, (ii) Community II, with many different gastropods, the most typical of which are *Clavatulula*,

Murex, *Ancilla*, *Conus*, *Cypraea*, *Tudicula*, *Strombus*, *Natica*, and representatives of the Nassariidae; as well as colonial corals, mainly *Tarbellastrea reussiana*, and (iii) Community III, which is generally similar to the preceding one but with some new taxa such as the bivalved gastropod *Berthelinia*, the chitons *Cryptoplax* and *Craspedochiton*, and the cirripede *Creusia*.

Community I *sensu* BAŁUK & RADWAŃSKI (1977) corresponds to the *Pteromeris*-coral assemblage *sensu* HOFFMAN 1977. The co-occurrence of *Dentalium badense* and *Flabellum* (typical of community I), recognised from five different localities in the Korytnica Basin (see Text-fig. 1 in BAŁUK 1972), indicates that community I occupied almost the entire study area. However, the absence of the *Pteromeris*-coral assemblage in almost all sections, with the exception of the Kar3 section (see Text-fig. 6), clearly shows that community I was characterised by a discontinuous distribution. The usefulness of the fossil communities distinguished by BAŁUK & RADWAŃSKI (1977) for the subdivision of the clays is thus clearly limited.

Fossil assemblages distinguished by HOFFMANN (1977) and recognised herein must also be excluded as a useful tool for subdivision of the Korytnica Clays because their succession varies distinctly within the basin (see Fig 6.).

Calcareous nannoplankton, dinoflagellate cysts and some benthic foraminifera recognised from the Korytnica Basin (see MARTINI 1977, GEDL 1996 and RÖGL & BRANDSTÄTTER 1993 respectively) allow correlation of the Korytnica Clays with other marine Miocene deposits, but do not enable their biostratigraphic subdivision.

Nassariid-based stratigraphy The succession of nassariid assemblages recognised in the Korytnica Clays allows subdivision of the succession into five ecostratigraphic units: Lower *restitutianus*, Lower *restitutianus-korytnicensis*, Upper *restitutianus*, *korytnicensis*, and Upper *restitutianus-korytnicensis*. This nassariid-based stratigraphy applies to almost the entire Korytnica Basin. The only exception is the littoral zone of the basin, which is characterised by the occurrence of the *schoenni* and *korytnicensis-limatus* assemblages (see Text-fig. 7).

The succession recognised herein allows correlation of the main exposures of the Korytnica Clays (see Text-fig. 6). Because some of the assemblages reappear twice in the succession (e.g. the *restitutianus* and *restitutianus-korytnicensis* assemblages) correlation based on isolated samples is usually impossible, and the presence of at least two successive assemblages is required for a reliable dating. The only exceptions are clays which contain

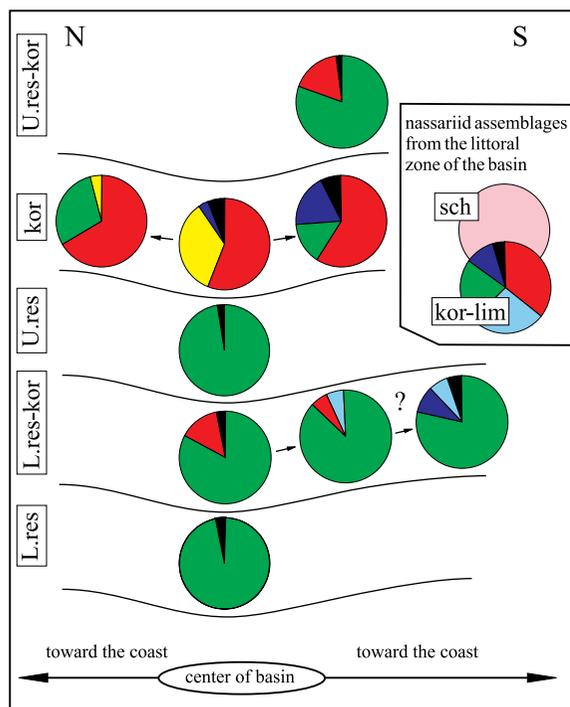


Fig. 7. Distribution of nassariid assemblages in the Korytnica Basin and nassariid-based stratigraphy of the Korytnica Clays. Ecostratigraphic units: L.res- Lower *restitutianus*, L. res-kor - Lower *restitutianus-korytnicensis*, U.res- Upper *restitutianus*, kor- *korytnicensis*, U.res-kor- Upper *restitutianus-korytnicensis*. Littoral nassariid assemblages: sch- *schoneenni* assemblage, kor-lim- *korytnicensis-limatus* assemblage. For taxonomic explanation see Text-fig. 2

the *korytnicensis* assemblage, as this appears only once, in the upper part of the succession.

Isochronous nature of the Upper *restitutianus/korytnicensis* boundary At the Upper *restitutianus/korytnicensis* boundary, *Nassarius restitutianus*, which predominated in the middle and lower parts of the succession, is partially or almost completely replaced by other nassariid species. *N. korytnicensis* replaces *N. restitutianus* within the whole study area, and in some parts of the basin *N. restitutianus* is also replaced by *N. styriacus* and/or *N. striaticosta*. The appearance of the *korytnicensis* assemblage is, in fact, the most significant change in the nassariid taxonomic composition recognised within the succession (see Text-fig. 6 and 7). The entry level of the *korytnicensis* assemblage is assumed here to be an isochronous surface. The postulated isochroneity is supported by the following observations: (1) the *korytnicensis* assemblage appears in the Korytnica Basin irrespective of the lithofacies. It occurs within sandy clay, clay with lenses of marl, and within clay lacking any distinct features (see Text-fig. 6). (2) the *korytnicen-*

sis assemblage appears irrespective of biofacies. It occurs in clays almost completely dominated by *Corbula gibba*, in sediments characterised by a substantial abundance of turritellids, as well as in those parts of the clay where the abundance of scaphopods is relatively high (see Text-fig. 6). (3) the Korytnica Basin is very small (ca. 4 km²) and during the middle Miocene there were no physical barriers within it (see WÓJCIK & SZYMANKO 1984). This means that the nassariids could spread within the basin rapidly and without any physical limitations. (4) The Upper *restitutianus/korytnicensis* boundary seems to reflect the bottom relief as it runs at a lower level in the centre of the basin and higher on its margins (see Text-fig. 8). (5) If the Upper *restitutianus/korytnicensis* boundary was really the bottom surface at some stage of development of the Korytnica Basin, its topographic position should also reflect the gentle inclination of the Korytnica Basin recognised by RADWAŃSKI (1969). In fact, such an inclination is recorded by the position of the boundary under discussion, as it runs 8-11 metres higher in the northern (Chomentów) than in the southern (Karsy localities) part of the basin (see Text-fig. 8). It must be emphasised that this slight difference cannot be explained by different bathymetric conditions because, in the marginal parts of the basin, the *korytnicensis* assemblage appears almost exclusively together with the same shallow water fauna dominated by *Turritella* (see Text-fig. 6).

In the light of the presented data the appearance of the *korytnicensis* assemblage in the Korytnica Basin was clearly rapid. However, the determination of the abiotic factors responsible for taxonomic changes observed at the Upper *restitutianus/korytnicensis* boundary is a much more complex problem.

The first, obvious explanation for the faunal replacement observed at the Upper *restitutianus/korytnicensis* boundary is a change in bathymetric conditions, because the whole sequence of the Korytnica Clays was interpreted by BAŁUK & RADWAŃSKI (1977) as formed in a progressively shallowing basin. Indeed, according to this well documented interpretation, there is no doubt that the *korytnicensis* assemblage appeared in the Korytnica

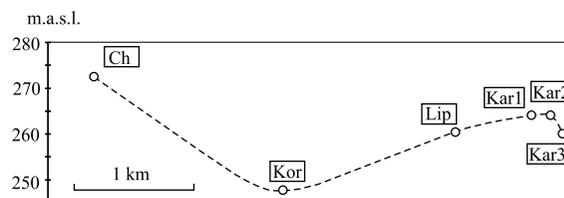


Fig. 8. Topographic position of the Upper *restitutianus/korytnicensis* boundary in the Korytnica Basin; m. a. s. l.- meters above sea level.

For localities - see Text-fig. 1

Basin when the depth of the water was relatively low. However, this simple explanation for the faunal replacement must be rejected because the *korytnicensis* assemblage appears in association with both the shallow water fauna characterised by the great abundance of *Turritella* and the fauna dominated by corbulids, indicative of a less energetic and therefore most probably somewhat deeper environment (this bathymetric interpretation of corbulid-dominated assemblages based on DAVITASHVILI & MERKLIN 1966 agrees with the central position of the assemblages observed in the Korytnica Basin, however Recent representatives of *Corbula gibba* from the Adriatic Sea also inhabit shallow-water environments – see ALLEFI & BETTOSO 2000). Moreover, a relatively high frequency of *Nassarius korytnicensis* is also observed in those parts of the basin that are characterised by the occurrence of oysters - bivalve molluscs typical of extremely shallow-water onshore environments (see Text-fig. 2). The co-occurrence of *N. korytnicensis* with different faunas suggests a relatively high bathymetric tolerance for this nassariid species. The appearance of the *korytnicensis* assemblage in the uppermost part of the succession should therefore be treated as coincidental in relation to the general shallowing of the basin and another explanation of the faunal replacement needs to be considered

The more likely explanation for the changes observed at the Upper *restitianus/korytnicensis* boundary is warming. The following arguments seem to support this hypothesis: (1) Recent representatives of many animal groups recognised hitherto from the entire sequence of the Korytnica Clays inhabit both the tropical and subtropical zones (for review see BAŁUK & RADWAŃSKI 1977 and references therein; see also SCHULTZ 1977; RADWAŃSKA 1984, 1992, RÖGL & BRANDSTÄTTER 1993). However, from the uppermost part of the clay characterised by the *korytnicensis* assemblage (from the topmost part of the Kar2 section), BAŁUK (1971) reported the polyplacophoran genus *Cryptoplax*, which is indicative of strictly tropical conditions. (2) In Recent communities, biodiversity is positively correlated with temperature (WEINER 1999). Those parts of the Korytnica Clays that contain the *korytnicensis* assemblage do indeed seem to contain be the most taxonomically diversified faunas, because *Cryptoplax* discussed above, is also a diagnostic species for community III, the highest diversity fossil assemblage recognised by BAŁUK & RADWAŃSKI (1977). The rough correlation of the *korytnicensis* assemblage with community III seems to be even more justified by the fact that the stratigraphic position of the *korytnicensis* assemblage within the whole study area (apart from the Kar3 section – see Text-fig. 6) agrees with the upper-

most position of community III, postulated by BAŁUK & RADWAŃSKI (1977).

The concept of climatic changes briefly presented above should be treated only as a preliminary hypothesis. However, if the latter argument is correct, it strongly supports the isochroneity of the Upper *restitianus/korytnicensis* boundary postulated herein.

Other boundaries As shown in Text-fig. 6, almost each section is characterised by its own, unique succession of macrobenthic assemblages. The most distinct sequence is observed within the Kar3 section because both the *Pteromeris*-coral and *Anadara* assemblages recognised there have not been reported from any other section. The same applies to the *Corbula*-spatangoid assemblage, as it appears exclusively within the Lip section. Moreover, even in that particular case, when the compared portions of deposits contain exactly the same fossil communities, their succession is also quite different – compare the relative position of the *Corbula* and *Corbula*-scaphopod assemblages within the Karsy (Kar2) and Lipa (Lip) sections (Text-fig. 6). The lack of any uniform sequence of macrobenthic fauna within the study area clearly indicates that particular parts of the basin were characterised by different environmental conditions during the sedimentation of the Korytnica Clays. In fact, the differences between the analysed successions are so significant that they suggest the occurrence of at least two or three different offshore environments at every stage of development of the Korytnica Basin.

Surprisingly, the succession of nassariid assemblages is identical within the entire study area. This indicates that their temporal and spatial distribution within the basin was not limited by local changes of the environmental conditions. The lack of any special environmental requirements seems to be displayed by all the nassariid assemblages recognised from the sections, as each of them appears in association with at least three different kinds of macrobenthic communities (see Text-fig. 2).

The low susceptibility of the nassariid assemblages to local changes in the environmental conditions undoubtedly favoured their rapid expansion over the entire area of the basin and should be treated as a serious argument for the possible isochroneity of all the boundaries investigated. The isochronous nature of the boundaries seems to be even more probable in view of the fact that all the nassariids were able to spread throughout the basin rapidly and without any physical limitations (for more details see previous paragraph).

The nature of changes in the nassariid taxonomic composition recorded below the Upper *restitianus/*

korytnicensis boundary also suggests that these changes occurred simultaneously throughout the study area. This is because the entire sequence of nassariid assemblages recognised in this part of the succession in fact reflects only more or less distinct fluctuations of the *N. korytnicensis*/*N. restitutus* ratio. It seems evident that this extremely simple succession should be interpreted as a record of temporal changes in the relative size of two large gastropod populations that inhabited almost the entire area of the Korytnica Basin. In a geological time scale such changes as described above occur rapidly, especially when the occupied area is small and there are no limitations for free gene flow within the population.

The succession of nassariid assemblages and the relation of the Korytnica Clays to the overlying members

The second appearance of the *restitutus-korytnicensis* assemblage was recognised only from the Karsy 3 section. In all the other sections the topmost part of the clays is occupied by the *korytnicensis* assemblage (see Text-fig. 6). The lack of the *restitutus-korytnicensis* assemblage in the topmost parts of most of the sections may suggest the occurrence of some depositional gap between the Korytnica Clays and the overlying marly sandstones. However, both GUTOWSKI (1984) and RADWAŃSKI (1969) have clearly shown that the sandstones overlie the clays concordantly, without any hiatus. In reality, the sandstones usually start to appear gradually in the uppermost part of the clays, forming a sort of a transitional bed. The second appearance of the *restitutus-korytnicensis* assemblage in the Kar3 locality may thus indicate that the deposition of clay within this part of the basin was longer than within the remaining study area. This means that the top of the Korytnica Clays (and consequently the base of the overlying marly sandstones) was most probably not a strictly isochronous surface.

ENVIRONMENTAL PREFERENCES OF NASSARIID SPECIES

The distribution of nassariid assemblages, taxonomic composition of the accompanying fauna and its palaeoecological interpretation enable determination of the environmental preferences of the six most abundant nassariid species occurring in the Korytnica Clays.

Nassarius schoenni inhabited poorly oxygenated coastal swamps situated in the southern marginal part of the Korytnica Basin (see BAŁUK & RADWAŃSKI 1977, HOFFMAN 1977). The relative frequency of this species at all other localities in the basin does not exceed 2% of the total number of nassariids in a sample.

Nassarius limatus occupied mainly the southern, littoral zone of the basin, characterised by very clear and turbulent waters. This marginal part of the basin was interpreted by RADWAŃSKI (1969) and HOFFMAN (1977) as an unprotected onshore environment. The relative frequency of *N. limatus* also reaches a significant value in sample 31, which probably represents a deeper littoral environment or one intermediate between a littoral and shallow-water environment; as well as in sample 38, taken from a deeper part of the basin. In general, the relative abundance of *N. limatus* seems to decrease rapidly toward the centre of the basin (see Text-fig. 7).

Nassarius striaticosta preferred shallow-water to littoral, high-energy environments and most frequently occupied the southern and south-eastern parts of the basin. Shallow-water areas inhabited by this species were characterised by a soft and fluid bottom, relatively clear water and the absence of marine plants. The bottom deposit was rather poor in organic matter. Environmental requirements displayed by *N. striaticosta* from the littoral zone of the basin are those that typify *N. limatus*. Although the shallow-water preferences of *N. striaticosta* are evident, the relative high abundance of this species in sample 16 (taken from the central part of the basin and containing the *Corbula* assemblage) indicates that it could also successfully inhabit deeper parts of the Korytnica Basin (see Text-figs 5, 7).

Nassarius restitutus occupied the entire Korytnica Basin and inhabited almost all environments recognised from the study area. It appears frequently in littoral, shallow-water and deeper parts of the basin. The only exception is the specific littoral zone (coastal swamps) entirely dominated by *N. schoenni*.

Nassarius korytnicensis inhabited numerous different environments and also occurred frequently within the whole Korytnica Basin area. Like the latter species, it was also absent in the littoral zone occupied by *Nassarius schoenni*. However, unlike *N. restitutus*, *N. korytnicensis* did not appear in sample 31. The taxonomic composition of this sample is interpreted here as indicative of a deeper littoral, or intermediate between littoral and shallow-water environment characterised by the occurrence of marine plants.

Nassarius styriacus preferred the central part of the basin with a bottom without seagrass cover. Water turbulence and turbidity did not affect the frequency of this species in any substantial matter. The relative abundance of this species in littoral and shallow-water environments is usually very low. The only exception is sample 9, where the relatively high frequency of *N. styriacus* is correlated with the occurrence of the shallow-water *Turritella* assemblage (see Text-figs 2, 5).

The succession of nassariid assemblages observed in the sections clearly shows that the relative frequencies of nassariid species varied not only in space but also in time. The relative abundances of *Nassarius korytnicensis*, *N. striaticosta* and *N. styriacus* reach their maximum value in the *korytnicensis* assemblage, which appears in the upper part of the clays. Other parts of the clays are dominated by *N. restitutus*, and only minor fluctuations of the *N. restitutus*/*N. korytnicensis* ratio are observed there (see Text-fig. 7).

If the hypothesis of climatic changes at the Upper *restitutus*/*korytnicensis* assemblages boundary presented above is correct, *Nassarius korytnicensis*, *N. styriacus* and *N. striaticosta* should be considered as typical of tropical conditions. Consequently, *N. restitutus* was most probably favoured cooler periods.

Apart from the taxa discussed above, nine other nassariids were recognised in the samples (see Table 1). However, their environmental preferences remain uncertain because their relative frequency is very low and they are usually represented by very few (often single) specimens. Because of this, their occurrence (or absence) in particular samples might be coincidental.

SUMMARY AND CONCLUSIONS

The analysis showed that the distribution of species of the family Nassariidae (Gastropoda, Prosobranchia) within the unbedded, homogeneous Middle Miocene Korytnica Clays is not uniform. Differences in the relative frequency of particular species allowed five nassariid assemblages to be distinguished. These are the *Nassarius restitutus*, *N. restitutus-korytnicensis*, *N. korytnicensis*, *N. korytnicensis-limatus* and *Nassarius schoenni* assemblages. The *schoenni* and *korytnicensis-limatus* assemblages occur only within single isolated localities corresponding to the southern, littoral zone of the basin. Other nassariid assemblages are characterised by a wide areal distribution within the basin and all of them occupied various offshore environments.

The succession of nassariid assemblages was identical throughout almost the entire area of the Korytnica Basin (except for the littoral zone). From the base of the clays to their top there appeared successively: the *restitutus*, *restitutus-korytnicensis*, *restitutus*, *korytnicensis* and *restitutus-korytnicensis* assemblages. The whole sequence seems to reflect temporal changes in the relative size of two large gastropod populations: the population of *Nassarius restitutus* and the population of *Nassarius korytnicensis*. The wide areal distribution and stability of this sequence was most probably related to the low susceptibility of these

nassariid species to local changes in the environmental conditions. Analysis of the fauna associated with both *N. restitutus* and *N. korytnicensis* clearly shows that they could have inhabited many different environments. The distribution of other common nassariids was controlled by bathymetry, water turbulence and turbidity as well as by the occurrence of marine plants.

The succession of nassariid assemblages recognised in the offshore parts of the basin enables correlation of the major exposures of the Korytnica Clays for the first time. The nassariid-based correlation seems to be very precise, as many geological and palaeobiological data indicate that the entry level of *korytnicensis* assemblage is an isochronous surface. The isochronous nature of the other boundaries between the nassariid assemblages, although less well documented, also seems probable.

The distribution pattern of nassariid assemblages also provides some information on the depositional history of the Korytnica Clays, suggesting that the sedimentation of the deposit in some small, southern part of the basin was longer than in the remaining study area.

Finally, the appearance of the *korytnicensis* assemblage reported from the upper part of the succession seems to be the most significant ecological event recognised hitherto from the whole sequence of the Korytnica Clays. The co-occurrence of some strictly tropical faunal elements and the broad correlation of the *korytnicensis* assemblage with community III, the most taxonomically diversified fossil assemblage distinguished from the clays by BAŁUK & RADWAŃSKI (1977), suggest that the appearance of the assemblage was caused by warming. If this preliminary hypothesis is correct, the whole succession of nassariid assemblages could be interpreted as a record of some climatic fluctuations that took place in the early Middle Miocene. This is because all changes in the nassariid taxonomic composition recorded from the succession are, in general, of the same nature as those related to the appearance of the *korytnicensis* assemblage. They also reflect the more or less distinct fluctuations of the *Nassarius restitutus*/*N. korytnicensis* ratio.

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