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Organic communities and facies development of the Korytnica basin (Middle Miocene; Holy Cross Mountains, Central Poland)

ABSTRACT: The Korytnica basin that developed during the Middle Miocene (Badenian) transgression onto the southern slopes of the Holy Cross Mountains, Central Poland, comprises a sedimentary sequence composed of the world-famous, much fossiliferous Korytnica Clays, and of overlying marly sands and red-algal (lithothamnian) limestones. The paleogeographic setting and the structure of the basin, being a part of the drowned valley, are discussed with a special attention to the littoral zone of the basin. This zone was featured with rubbles and abrasion surfaces, all of which are densely bored by diverse rock-borers (sponges, polychaetes, pelecypods, acrothoracican cirripedes). Special littoral facies are exemplified by the oyster shellbed, and sandy clay with brackish gastropods, the latter of which is interpreted as confined to coastal swamps of the mangrove type. The main facies of the basin, the Korytnica Clays, is discussed in regard with its sedimentary conditions, taphonomy of the fossils and their burial conditions. The most important organic communities and their vertical succession are presented, and a conclusion on the seagrass vegetation in the basin is drawn. Discussed are also some biological relationships between the particular species, and results of the activity of hermit crabs upon alive mollusks. The decline of sedimentation in the basin manifested with the extreme shallow marine facies that correspond to a complete filling of the basin with sediments up to sea level. The climatic conditions that prevailed in the Korytnica basin are characterized as very close to those typical of present-day tropical and/or subtropical zones. Finally, the Indo-Pacific elements within the Korytnica assemblages are indicated, and a discussion on the connections of the Miocene sea of Europe with the Indo-Pacific province is presented.

INTRODUCTION

The aim of the present paper is to show the recent results of investigations on the diversified fossils and their assemblages from the world-famous Middle Miocene (Badenian) Korytnica Clays. These famous

clays developed within the Korytnica basin on the southern slopes of the Holy Cross Mountains in Central Poland, and the sedimentary sequence of that basin comprised also other facies, all of which are much fossiliferous. The fossils from all these facies are commonly regarded as the Korytnica fossils, and under such a name are known in many European collections.

The own research undertaken by the authors in the sixties resulted in the recognition of general facies conditions prevailing in the basin (Radwański 1964, 1969), and of the littoral ichnocoenoses (Radwański 1970, 1977b); in the monographing of a part of the mollusks, being the most common fossils in the clays, viz. chitons (Bałuk 1971), scaphopods (Bałuk 1972), and archaeogastropods and some caenogastropods (Bałuk 1975); as well as in the special studies on such unique fossils as the creusoid barnacles domiciled in corals (Bałuk & Radwański 1967), and the bivalved sacoglossan gastropods (Bałuk & Jakubowski 1968). Moreover, during the collecting work, many new groups have been recognized and delivered to the specialists from various countries.

The results of the completed studies on some groups are included into this issue of ACTA GEOLOGICA POLONICA (Vol. 27, No. 2; Warsaw 1977). It comprises the reports on calcareous nannoplankton and its stratigraphical importance (Martini 1977), on some large-sized foraminifers (Walkiewicz 1977a), brachiopods (Barczyk & Popiel-Barczyk 1977), free-living bryozoans (Bałuk & Radwański 1977), cuttlefish (Bałuk 1977), holothurians (Walkiewicz 1977b), echinoids (Mażyńska 1977), and some fish (Schultz 1977). Moreover, presented are reports on large pinnid pelecypods (Jakubowski 1977), and burrows attributable to the ghost crabs (Radwański 1977a), both coming from the deposits overlying the clays, and finally, a larger paper on the synecology of macrobenthic assemblages from the clays (Hoffman 1977) fills up this issue. Some other collected groups of the invertebrate fossils are either under investigation (small foraminifers, corals, tubular polychaetes, bryozoans, cirripedes, crabs, pelecypods, crinoids, fish otoliths), or ready for the research (ostracodes, ophiuroids, starfish). If these studies are successful in the forthcoming future, the next issue on the Korytnica fossils will be kindly offered to the readers.

PALEOGEOGRAPHIC SETTING OF THE BASIN

The Korytnica basin of Middle Miocene (Badenian) age is a small, c 5 sq km terminal part of a larger bay, the Korytnica Bay (cf. Text-figs 1—2), which developed during the Middle Miocene transgression on the southern slopes of the Holy Cross Mountains in Central Poland. This transgression was confined to the area of the Fore-Carpathian

Depression (cf. Text-fig. 1B), the development of which had controlled the marine invasion from the Vienna Basin and the Mediterranean (cf. Text-fig. 1A).

The Fore-Carpathian Depression, situated at the northern margin of the Carpathians (cf. Text-fig. 1A—B), is bordered to the north by the Central Polish Uplands (Polish Jura, Cracow and Miechow Uplands, Holy Cross Mts, Lublin Upland — cf. Text-fig. 1B). In a geotectonic sense, these uplands form the circum-Carpathian belt which was elevated as an isostatic response to Carpathian folding and formation of the Carpathian foredeep. The evolution of this foredeep, viz. the Fore-Carpathian Depression, took place in a relatively short time in the Middle Miocene, when the Badenian marine invasion entered this and incorporated it into a system of circum- and intra-Alpino-Carpathian basins, commonly called the Paratethys basins (*d* in Text-fig. 1A), as they originated from the Tethys Ocean of Mesozoic-Paleogene time.

Towards the east, the Middle Miocene (Badenian) transgression reached the western Ukraine. The latter region was very close to the Euxinian Basin (*e* in Text-fig. 1A) which belonged to the Euxino-Caspian province characterized by more or less lagoonal development with weak connections to the Paratethys basins. Another separate system of basins existed at that time in western Europe where a few Atlantic gulfs (*b* in Text-fig. 1A) encroached upon the continent, and the North Sea Basin developed wider than now (*a* in Text-fig. 1A) and having a temporary at least connection to the Atlantic Ocean through the English Channel (cf. Martini 1974). On the other hand however, the North Sea Basin had evidently no connection with the Paratethys basins of which the Fore-Carpathian is the northernmost (see *B* in Text-fig. 1A); although unjustified opinion on the existence of such a connection was once expressed by von Linstow (1922) and commonly repeated by subsequent authors (Kautsky 1925a, b; Sorgenfrei 1940, p. 88, and 128; 1958, p. 9; cf. discussion in Friedberg 1930; Gignoux 1955, pp. 592—593 and footnote on p. 603).

The triangular shape of northern limits of the Fore-Carpathian Depression (cf. Text-fig. 1A—B) results from deep fractures in the Earth crust. The eastern limb, along the Lublin Upland, parallels the SW margins of the Fenno-Sarmatian Shield, being in this part the Ukrainian Platform, and it also parallels the axis of the Danish-Polish Trough (cf. Kutek & Głazek 1972). The western limb of this triangle supposedly reflects another fracture, more or less perpendicular to the former, both of them being established during evolution of the Danish-Polish Trough, and renewed during development of the Carpathian foredeep.

During the Middle Miocene (Badenian) transgression both these limbs were controlling the general extent of the sea which entered the slopes of the Central Polish Uplands along the valleys. The terrestrial erosion took here place in Paleogene after the Laramide folding of the Danish-Polish Trough and during successive uplift of the area (cf. Kutek & Głazek 1972). Vadice erosion of surface waters was then accompanied by chemical corrosion of carbonate belts which readily underwent strong karstification in tropical or subtropical climate of the Eocene (cf. Głazek, Dąbrowski & Gradziński 1972). The valley network was transformed during the transgression into a diversified system of bays with differentiated shoreline, the extent of which is recognizable in the present-day morphology by occurrences of various littoral structures. This is the best demonstrated along the southern slopes of the Holy Cross Mountains, especially in their western part where the Korytnica basin is located (cf. Text-fig. 1B—C).

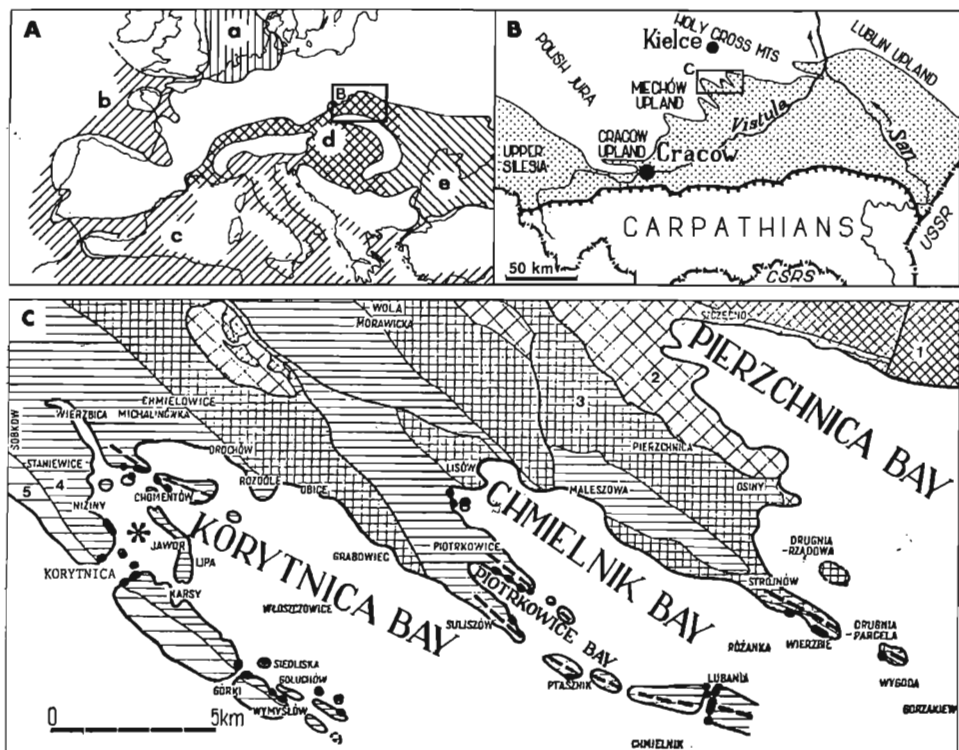


Fig. 1. Paleogeographic setting of the Korytnica basin

A — Marine basins in the Middle Miocene of Europe: a North Sea Basin, b Atlantic gulfs (Brittany, Touraine and Anjou Basin, Aquitanian Basin, Lisbon Basin), c Western Mediterranean Basin (= Tethys Basin), d Paratethys basins, e Euxinian Basin; reangled is the area enlarged in Text-fig. 1B
 B — Extent of the Middle Miocene (Badenian) sea in the Fore-Carpathian Depression (stippled); reangled is the area enlarged in Text-fig. 1C
 C — Middle Miocene (Badenian) shoreline and extent of the bays on the southern slopes of the Holy Cross Mountains; preserved localities of littoral structures are marked with black spots along the shoreline; asterisked is the Korytnica basin (cf. Text-fig. 2) situated in the terminal part of the Korytnica Bay (cf. Radwański 1969, Fig. 25; 1970, Fig. 1)

Within the inland areas distinguished are the occurrence zones of: 1 Cambrian (including locally Ordovician and Silurian), 2 Devonian, 3 Triassic, 4 Jurassic, 5 Cretaceous; marked with heavy dashes are the ridges in morphology that separate particular bays

The valley network was here established mostly along the strike of the Laramide folds (cf. Text-fig. 1C; and Kutek & Głazek 1972), built up primarily of the Devonian and Mesozoic carbonate rocks. As result a Dalmatian-type of the shoreline developed in which extensive bays along previous valleys are the typical feature, and these are separated by more or less pronounced rocky ridges (cf. Text-fig. 1C). The mechanical abrasion along the shore produced here such diverse littoral structures as cliffs, cliff rubble, and abrasion surfaces or platforms, all of them having been densely populated by usually gregarious rock-borers (cf. Radwański 1964, 1969, 1970, 1974).

Within the so-developed bays, the marine Middle Miocene (Badenian) sedimentation mostly consists of various limestones and marls, the origin of which resulted from profuse red-algal vegetation. As most of these bays were extensive

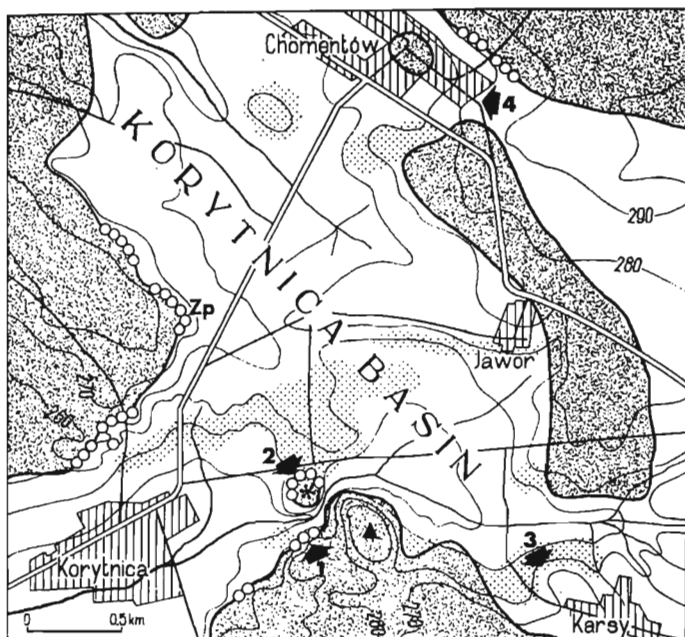


Fig. 2. Paleoenvironmental sketch of the Korytnica basin

Indicated are: marine area of the Korytnica basin during the Middle Miocene (Badenian) transgression (blank) and present-day outcrops of the Korytnica Clays (stippled); preserved fragments of littoral structures (circled); land or island areas along the seashore (hachured)

Asterisked is the summit of Mt. Lysa; marked with black triangle is the summit of Mt. Grodzisko (cf. Text-fig. 3)

Numbered are some more important localities discussed in the text:

- 1 — North-western slopes of Mt. Grodzisko: littoral rubble with borings domiciled by secondary dwellers (*Sphenia*, *Striarca*, *Crepidula* — see Pl. 1, Figs 1–5); clay facies with brackish gastropods. This is the area of conjectured mangrove swamps (cf. Text-fig. 5), discussed i.a. by Radwański (1969, 1974) and Hoffman (1977)
 - 2 — Northern slopes of Mt. Lysa: littoral rubble covered by oyster shellbed (lumachelles) containing diverse fossils (cf. Text-fig. 5) described by previous authors
 - 3 — The only natural exposure of the Korytnica Clays, situated on the northern slope of the hill capped by the village Karsy; this is the locality often named by previous authors as Karsy
 - 4 — Sand pit at Chomentów where the deposits overlying the Korytnica Clays are exposed: these are marly sands and red-algal (lithothamian) limestones, both containing diverse fossils (cf. Radwański 1969, Text-fig. 33; 1970, Text-fig. 4; 1977a, b; Jakubowski 1977)
- Zp — Biotope of the acrothoracican barnacles, *Zapfella pattei* Saint-Seine, within the littoral rubble and fragmentary abrasion surface (cf. Pl. 1, Fig. 6)

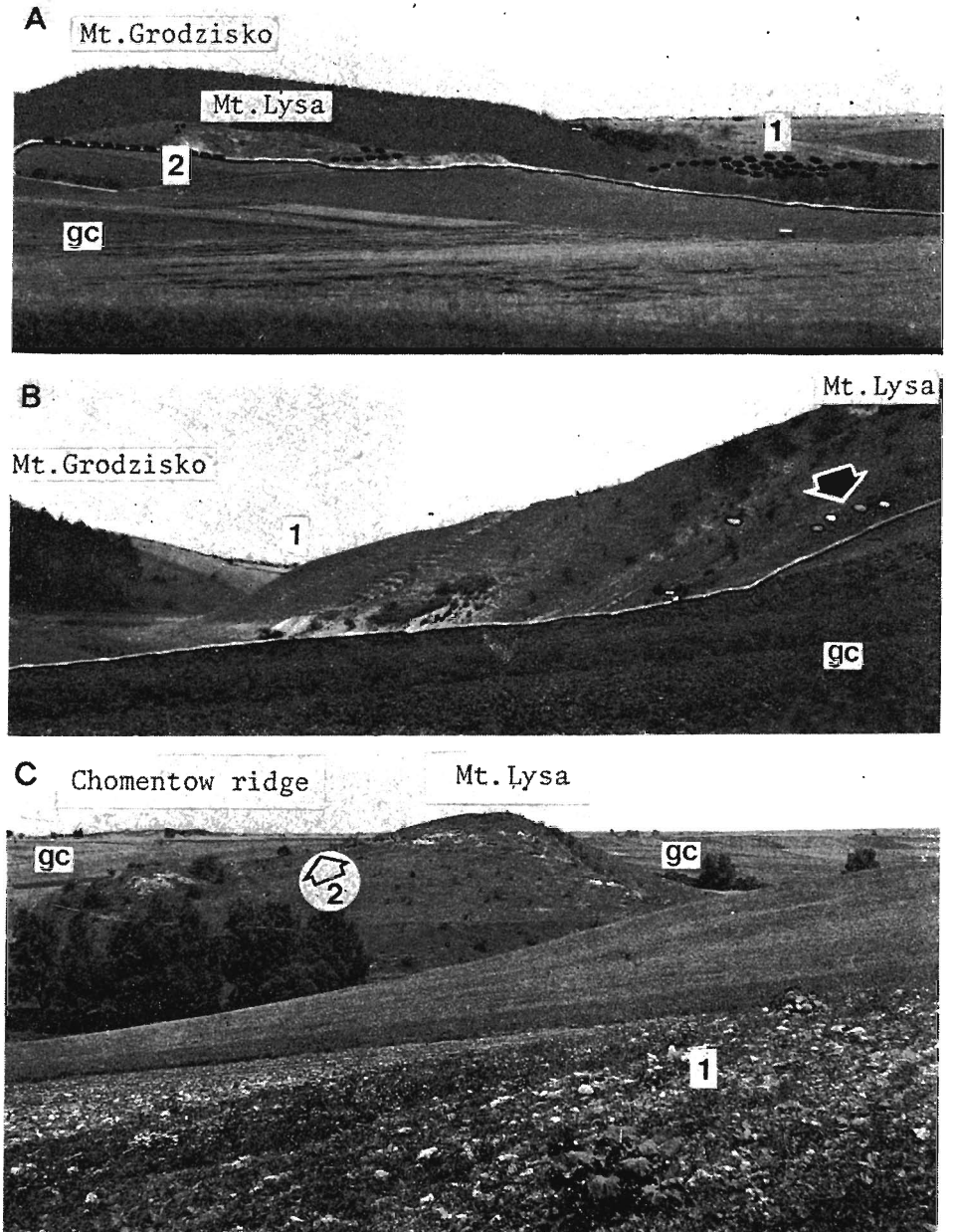


Fig. 3. Present-day topography along the Middle Miocene (Badenian) shoreline of the Korytnica basin (cf. Radwański 1969, Pl. 33; Bałuk 1975, Text-fig. 5)

A — View from the village Korytnica (see Text-fig. 2) to localities 1 and 2 of the littoral structures (littoral rubble marked with black spots); indicated is also the present-day extent of the gastropod-bearing clays (gc)

B — View at the pass between Mt. Lysa and Mt. Grodzisko (cf. Text-fig. 2); at the background visible is the area of locality 1; arrowed are fragments of abrasion surface and littoral rubble; indicated is also the present-day extent of the gastropod-bearing clays (gc)

C — View from locality 1 to Mt. Lysa (cf. Text-fig. 2); locality 2 is arrowed, and areas of the gastropod-bearing clays (gc) exposed over the cropland are indicated; in the background visible is the Chomentow ridge bounding the Korytnica basin from the north (cf. Text-fig. 1C and 2)

but shallow, and their bottoms were situated within the range of the photic zone, diverse species of the red alga *Lithothamnium* could thrive here and supply detrital material to various local deposits. Of these, the most common are pure or marly lithothamnian limestones, and lithothamnian marls composed of algal nodules in the marly matrix.

The only exception of such sedimentation type was the Korytnica Bay which was the deepest of all the discussed bays. Both clastic and lithothamnian deposits were laid down in the open part of the bay, whilst at its terminal, westernmost part, behind a submerged ridge a restricted basin had formed. This is the Korytnica basin (cf. Text-figs 1C and 2) in which clay material, presumably supplied by a stream or a river from the weathered residues of the Jurassic (Kimmeridgian) clays and marls, was deposited through almost the whole history of the basin: the world-famous Korytnica Clays that contain the extreme wealth of various fossils then originated. Sedimentation of marly sands and lithothamnian limestones appeared in the basin by the decline of its history and it completed the sequence of the so fossiliferous strata.

Contrary to the region of bays, the eastern part of the Holy Cross Mountains was at that time featured mostly by sandy sedimentation. The clastic material was then supplied from the old Paleozoic (primarily Cambrian) clastics, and sandy shores could widely develop (cf. Radwański 1970, 1973, 1974).

Within such paleogeographic situation, the Korytnica basin provided a unique framework to the appearance of very specific facies conditions that resulted both in uncommon sediment types, and in the wealth of diversified organic remains they contain.

STRUCTURE OF THE BASIN AND ITS SEDIMENTARY SEQUENCE

The Korytnica basin developed in the part of the bay which was bordered from the north by a ridge built up of massive Oxfordian limestones, and from the south, by another ridge built up of Lower/Middle Kimmeridgian limestones and clays covered penecordantly with Albian/Cenomanian compact sandstones that form the top part of this ridge (cf. Text-figs 1C and 2). To the east, another, presumably submerged ridge separated the basin from the open part of the bay. All these ridges were cut by straits which joined the basin with the other parts of the bay, and with the open sea to the south, which allowed exchange of water. In result, normal marine conditions prevailed in the basin, and except of some restricted areas, no oligohaline conditions could persist.

The Middle Miocene (Badenian) sedimentary sequence of the basin (cf. Text-fig. 4) begins with local accumulations of the brown-coal deposits, not exposed at the surface. The main part of the sequence consists of the Korytnica Clays, the thickness of which depends on local denivelations of the substrate, and reaches 40 to 60 m. Overlying are sandy marls and lithothamnian limestones, the total thickness of which is about 10 m. The presented figures of the deposit thicknesses are estima-

tive as it is also apparent that a lateral facies variation took place during sedimentation of the members overlying the clays (cf. Radwański 1969).

The Middle Miocene (Badenian) sequence lies in the basin flat (cf. Text-fig. 4), evidencing no tectonic movements except of an isostatic upheaval of the whole basin. Local deformations of some compact layers of marly sands are ascribed to uneven compaction.

The present surface that results from Late Tertiary and Quaternary erosion, incises various parts of the clays and removes them from the more elevated substrate hummocks making them exposed (cf. Mt. Lysa in Text-figs 2 and 4—5).

Within the Korytnica Clays there are no larger exposures, except one at the village Karsy (cf. locality 3 in Text-fig. 2). All the paleontological material from the clays is obtained from trenches and local diggings, and from collecting the fossils over the cropland (cf. Text-fig. 3C), especially after spring or fall plowing, the same as after every heavier rainfall. In last years it appeared that the ablation and resulting concentration of fossils in the soil does not keep up with the acquisitiveness of the collectors.

The westernmost part of the basin stretches with a narrow embayment as far as the village Wierzbica (cf. Text-fig. 1C) where the Korytnica Clays have been preserved in some spots and delivered the same fossils as those from the basin (cf. Kowalewski 1930; Radwański 1967, 1969).

STRATIGRAPHY

The sedimentary sequence of the Korytnica basin was formerly regarded as belonging to the lower part of the Polish Tortonian which was correlated exactly with the Vienna Tortonian (cf. Radwański 1969, 1973, 1974 a, b). Within the stratigraphic column of the Polish Tortonian, there were distinguished two substages, the lower of which (Opolian) comprised a full sedimentary cycle ranging from the transgressive deposits through the final evaporation and formation of gypsum deposits. In such a subdivision, the Korytnica sequence was placed in the lower part of the cycle, i.e. in the Lower Opolian (cf. Radwański 1969, 1974a).

When new stratigraphic division of the Vienna Tortonian was established, no evident correlations were presented, although it was generally believed that the Polish Tortonian should correspond to the new established Badenian stage of the Vienna Basin.

The first account on the reliable stratigraphic correlations is now presented by Martini (1977) who recognized in the calcareous nannoplankton from both the Korytnica Clays and overlying marly sands, the presence of standard nannoplankton zones NN5 (*Sphenolithus hetero-*

morphus Zone) and NN6 (Discoaster exilis Zone). In result, Martini (1977, Text-fig. 3) demonstrates that the Korytnica sequence is correlatable with the upper part of the classical section of clays at Sooss, and with the lower part of the Walbersdorf section in the Vienna Basin. When taking into account the current biostratigraphic subdivision of the Central Paratethys Miocene (Steininger, Rögl & Martini 1976), it is evidenced by Martini (1977) that the Korytnica sequence is the equivalent to the middle part of the Vienna Badenian, and to the upper part of the type Langhian in Italy; it cannot be in any case correlated with the type Tortonian of Piedmont in which much younger nannoplankton zones (NN9 — NN11) are present (cf. also Martini 1975; Steininger, Rögl & Martini 1976).

THE LITTORAL ZONE OF THE BASIN

The littoral zone of the Korytnica basin is shaped mostly by littoral rubbles encountered on the slopes of the shore, along which small areas of abrasion surfaces developed locally (cf. Text-figs 2—3). Usually, abrasion surface was formed in parts of the shore where more compact and resistant limestones were exposed, whereas the layered limestones were transformed into the littoral rubble (cf. Text-figs 3 and 5). All these littoral structures are densely bored by diverse rock-borers, among which the most important are (cf. Radwański 1964, 1965a, 1969, 1970): sponges *Cliona celata* Grant and *C. vastifica* Hancock; polychaetes *Potamilla reniformis* (O. F. Müller), *Polydora ciliata* (Johnston) and *P. hoplura* (Claparède); pelecypods *Gastrochaena dubia* (Pennant), *Aspidopholas rugosa* (Brocchi), *Jouannetia semicaudata* (des Moulins), and *Lithophaga lithophaga* (Linnaeus); and acrothoracican barnacles *Zapfella pattei* Saint-Seine. All these rock-borers are very common, locally even gregarious, in all the sites of littoral structures (cf. Pl. 1), except of the acrothoracican barnacles *Zapfella pattei* Saint-Seine which appear in greater quantities only in one place (marked Zp in Text-fig. 2; cf. Pl. 1, Fig. 6).

Of these rock-borers a special attention is to be paid to pelecypods whose shells, or internal moulds, are sometimes preserved within the borings. They allow to determine both the boring species, and to ascribe the empty borings to particular species as the morphology of the borings strictly corresponds to that of the shells (cf. Radwański 1965a, 1969, 1970, 1977b). The most common material within the ichnocoenose, the empty borings of the pelecypods, may therefore be well ascribed to normal body-fossil species. All the remaining taxa of the borings fall into the category of trace fossils.

When comparing the composition of the littoral ichnocoenoses of the Korytnica basin with those of the open-sea parts of the Korytnica

bay, and of other regions of the Holy Cross shores, it is evident (cf. Radwański 1969, 1970) that some rock-borers (mostly echinoids) are missing in this protected part of the bay, and others (e.g., polychaetes *Polydora hoplura*, and pelecypods *Lithophaga lithophaga*, especially their larger forms) are much less frequent here. These differences resulted from hydrodynamic conditions within the particular biotopes and from biological requirements of these rock-borers (cf. Radwański 1969, 1970).

INHABITANTS OF EMPTY BORINGS

Many of the empty pelecypod borings within the littoral rubbles, especially those at the locality 1 (cf. Text-figs 2—3 and 5) were domiciled by various secondary dwellers whose shells remained preserved (cf. Pl. 1, Figs 1—5), the same as of primary rock-borers (cf. Pl. 1, Fig. 3). The squatters of empty borings are mostly (cf. Text-fig. 5; and Radwański 1969, 1970, 1974 a, b) pelecypods *Sphenia anatina* (Basterot) and *Striarca lactea* (Linnaeus), the latter of which has a similar mode of life in present-day environments in the Adriatic and Black Sea (cf. Starmühlner 1963a, Nevevskaya 1965). Less frequent are the gastropods, the slipper limpets *Crepidula crepidula* (Linnaeus), which more commonly occur as secondary dwellers of any empty shells within the Korytnica Clays (cf. Pl. 2, Fig. 15; and Radwański 1969, 1974b).

All these squatters of empty borings adopted their shape to that of the borings regardless their outline corresponding to diverse rock-boring pelecypods. In result, the shape of the squatters is much variable and deviated from the "standard" forms of particular species. Sometimes, it was also dependant upon the space left by the original rock-borer whose shell remained preserved in the boring during the life

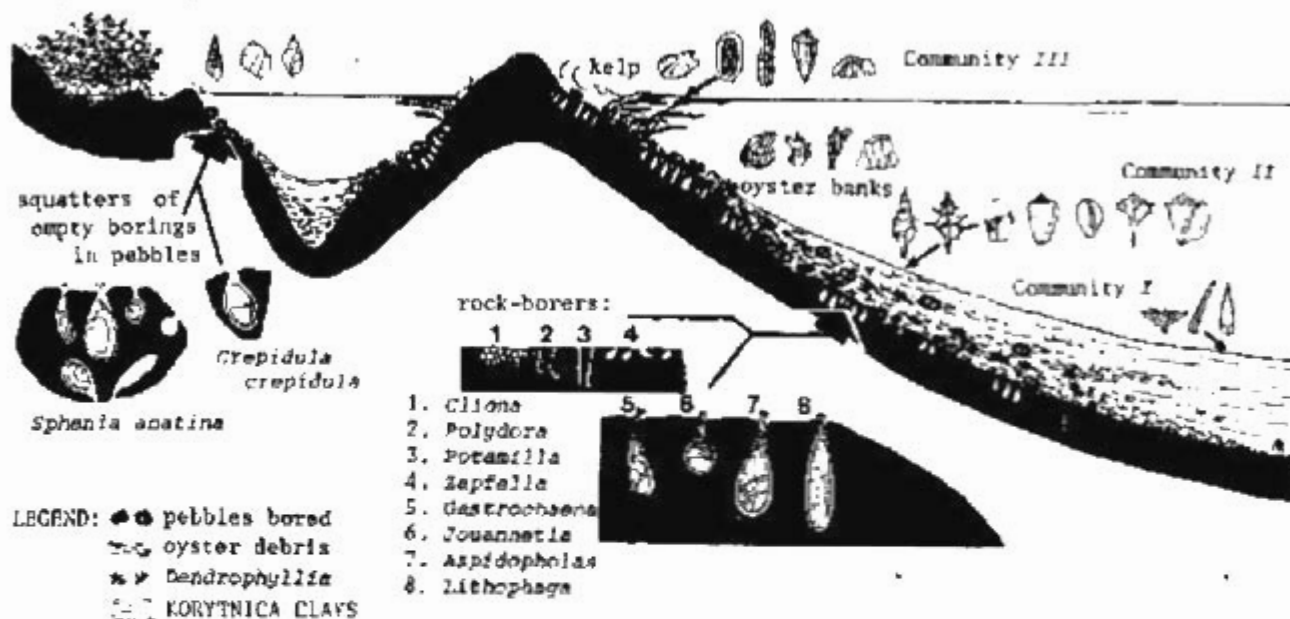
KORYTINICA

CHOMENTOW



Fig. 4. Idealized section through the Korytnica basin (not to vertical scale; cf. Text-fig. 2) to show the general sequence of the Middle Miocene (Badenian) deposits
 1 brown-coal deposits, 2 KORYTINICA CLAYS, 3 marly sands, 4 red-algal (lithothamnian) limestones

Mangrove swamps



Idealized shorescape to show the distribution of organic communities at rocky seashores of the
 Korytnica basin

Community I: coral *Flabellum*, sesshopod *Dentalium badense*, gastropod *Turritella*

Community II: gastropods *Clavata*, *Murex*, *Ancilla*, *Comus*, *Cypraea*, *Fadula*, *Strombus*, the large-sized forms of *Triton*, *Conus*, *Cypraea*, *Strombus*, *Murex*, *Xenophora*, *Rostellaria*, and *Galeodes* including (cf. Pls 7-8); colonial corals *Tarbellastraea*; activity of various littoral rock borers (cf. Pls 3-5), and of hermit crabs (cf. Pls 16-17)

Community III: the same as II, but with participation (cf. Pl. 9) of bivalved gastropods *Berthelina*, ebtons *Craspedochiton* and *Cryptar*, cirripedes *Crasia* (domiciled in corals *Tarbellastraea*), *Verruca* and *Citharus*, as well as of free-living bryozoans (cf. Bak & Radwański 1977)

Oyster bank community: *Ostrea frondosa* associated with corals *Dendrophyllia*; cirripedes *Scalpellum*, *Balanus* and *Anassa*; gastropods *Lentidium arenaria* (Linnaeus) and *Tenagodus*

Community of brackish pools and mangrove swamps: gastropods *Terebralia*, *Neritina* and *Melanopsis*; secondary dwellers, pelecypods *Sphania anatina* (Pasterot) and *Striarca lactea* (Linnaeus), and gastropods *Crepidula crepidula* (Linnaeus), domiciled in empty borings within the littoral rubble (cf. Pl. 1, Figs 1-3)

of a squatter (cf. Pl. 1, Fig. 3; *Sphenia anatina* adopted to the shell of *Jouannetia semicaudata* preserved in its boring).

OYSTER SHELLBED

The oyster lumachelles, composed of various shell detritus, mostly of the oyster *Ostrea frondosa* de Serres and other pelecypods associated with gastropods, and contained in marly matrix, are a local littoral facies (cf. Friedberg 1928, 1931; Radwański 1964, 1969). This facies is best developed on the slopes of Mt. Lysa which made up an island during sedimentation in the Korytnica basin (cf. Text-figs. 3—5). On the northern slopes of Mt. Lysa, there appears the only exposure of this facies which covers a littoral rubble, as it is visible in a small abandoned quarry (locality 2 in Text-fig. 2; cf. also Text-fig. 3A and C).

The oyster lumachelles form a kind of the oyster shellbed (os in Text-fig. 6) which was accumulated simultaneously with the deposition of the Korytnica Clays further off the island shore. The oyster material vanishes at the distance of c 30—50 m off this shore, and the deposit gradually becomes the gastropod-bearing Korytnica Clays (cf. Text-fig. 3A).

Although now the oyster shellbed wraps up the whole island of Mt. Lysa (cf. Text-fig. 6), the oyster banks during sedimentation were certainly developed locally, mostly amidst elevations of the substrate which, being more exposed, became habitats for the rock-borers (cf. Text-fig. 5). In other parts of the shore slope the seagrass carpets then also occurred (cf. Text-fig. 6).

A rich community of the oyster banks comprises also (cf. Text-fig. 5) diverse corals, mostly *Dendrophyllia taurinensis* Milne-Edwards & Haime, *Balanophyllia varians* Reuss, and others (cf. Dembińska-Rózkowska 1932, Kühn 1963), as well as cirripedes of the genera *Scalpellum* Leach, *Balanus* da Costa and *Acasta* Leach, the first two were supposedly attached to the oysters, whereas the third one lived inside the sponges (cf. Bałuk & Radwański 1967, p. 498; Radwański 1969, p. 90). Associated are various serpulids (Bałuk 1975), and gastropods, of which typical are *Lemintina arenaria* (Linnaeus) and *Tenagodus*, both discussed below.

MANGROVE COAST

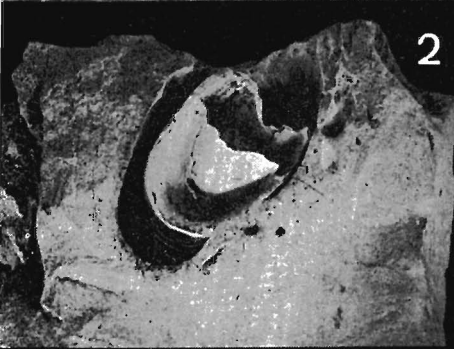
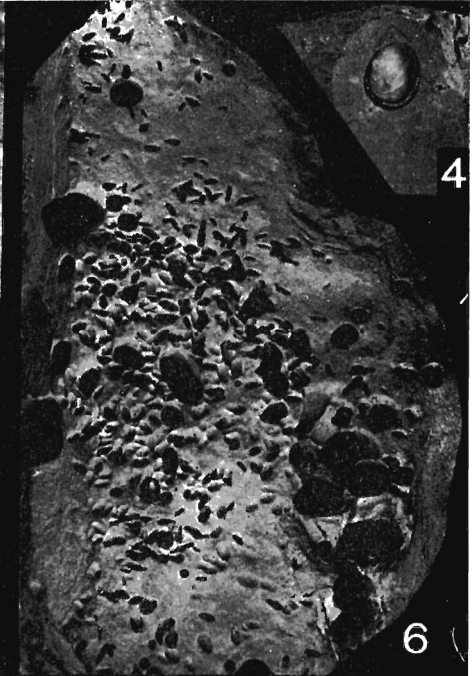
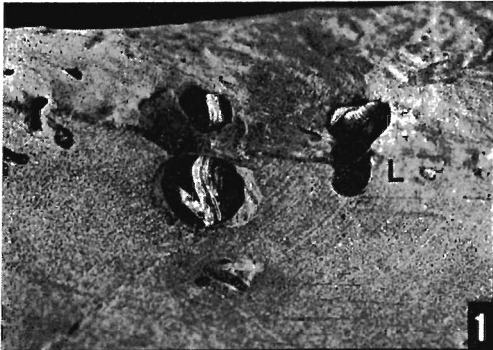
Another littoral facies of a local development is the clay with greater admixture of quartz sand, and containing commonly some gastropod species which are either rare or missing in the main area of the Korytnica Clays. This sandy clay is exposed only on the north-western slopes of Mt. Grodzisko (locality 1 in Text-figs 1—2), and it covers a littoral rubble with the above-discussed secondary dwellers of empty pelecypod borings.

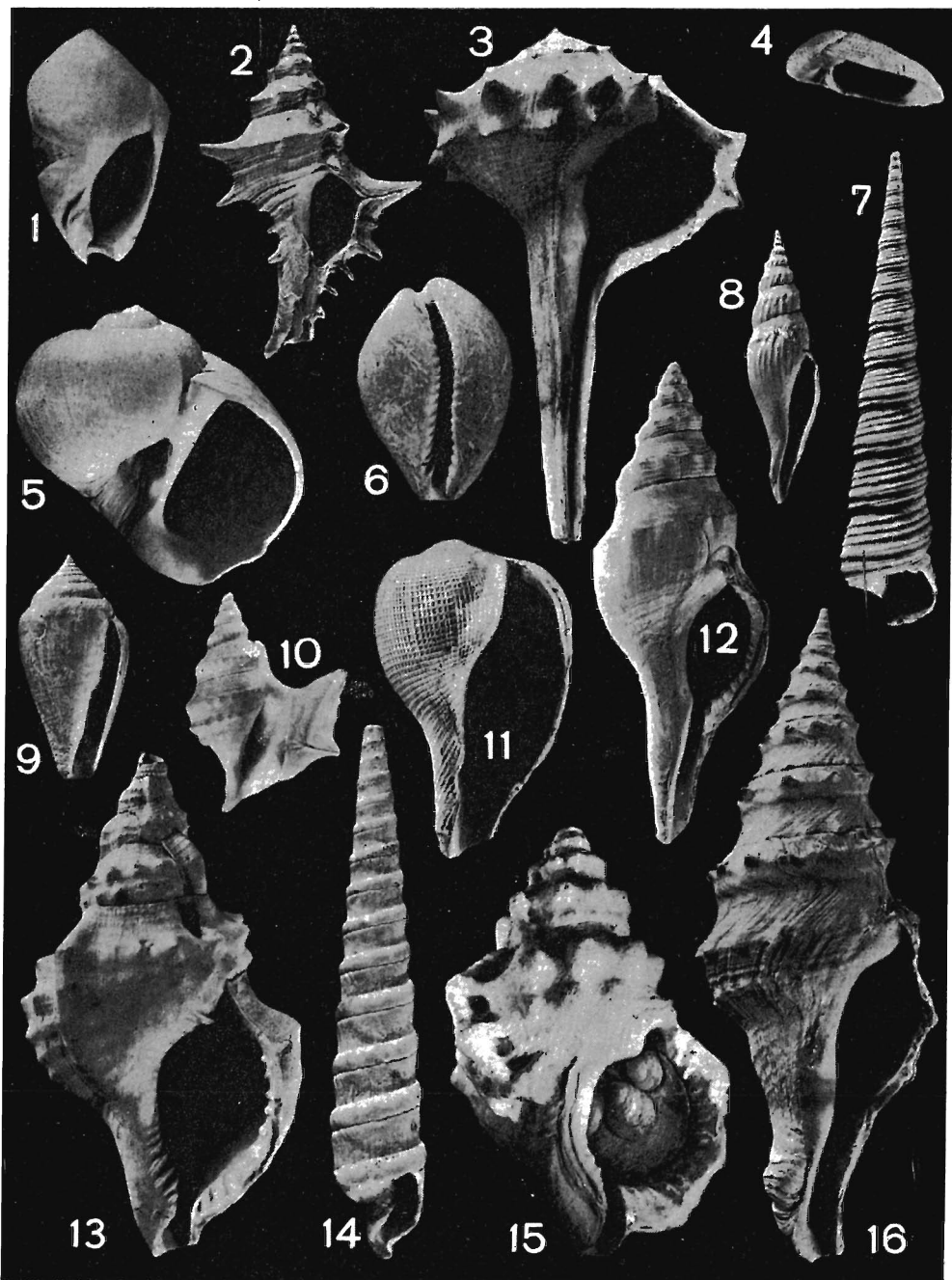
The gastropod species such as *Terebralia bidentata* (Grateloup), *Pirenella tabulata* (Hörnes), *Cerithium* aff. *zelebori* Hörnes, *Neritina picta* Férussac, and *Melanopsis aquensis* Grateloup, are of typical brackish character. Their occurrence here (cf. Text-fig. 5) may be explained by special paleogeographic conditions that controlled a local development of the restricted environment. It was a part of the shore of the ridge (cf. Text-figs 1C and 2) that was facing the island of Mt. Lysa (cf. Text-figs 2—3). The water agitation and circulation were here certainly weaker, which explains the preservation of some shells of rock-boring pelecypods, and of secondary dwellers within the emptied borings (cf. Radwański 1969, 1974). On the other hand, the morphology of the discussed ridge featured with broad denivelations that paralleled marly horizons within the Jurassic substrate, produced a notchy shoreline with differentiated facies conditions. The terrestrial material, both clayey and sandy, was easier accumulated here, and it blurred and covered quickly the rocky substrate. It was suggested (Radwański 1974) that under such conditions the coastal swamps could develop, and they were overgrown by mangrove-type thickets (cf. Text-fig. 5). In such a spot, a protected environment might have been established amidst the quaggy ponds and the maze of prop roots (cf. Plaziat 1970, Taylor 1971, Braithwaite & al. 1973), and the brackish conditions prevailed even if the fresh-water supplies from the discussed ridge have not been immense (cf. also Plaziat 1975 a, b).

The above interpretation on the occurrence of mangrove swamps (cf. also Hoffman 1977) is partly based on that presented by Braithwaite & al. (1973) for some members of the Quaternary sequence of the Aldabra Atoll, Indian Ocean, where the presence of *Terebralia* and other

PLATE 1

- 1—5 — Squatters of empty borings in pebbles making up littoral rubble at Korytnica (locality 1 in Text-fig. 2; cf. also Text-fig. 5)
- 1 Gastropod *Crepidula crepidula* (Linnaeus) adapted to the boring of *Gastrochaena*; at right, pelecypod *Striarca lactea* (Linnaeus) squats another boring (marked L); $\times 1.5$
 - 2 Gastropod *Crepidula crepidula* (Linnaeus) adapted to the boring of *Lithophaga* provided with a crest corresponding to the hinge margin of the boring shell (cf. Radwański 1969, Pl. 35, Fig. 8); $\times 1.5$
 - 3 Gastropod *Crepidula crepidula* (Linnaeus) adapted to another boring of *Lithophaga*; above, pelecypod *Sphenia anatina* (Basterot) squats (marked S) a small boring of *Jouannetta semicaudata* (des Moulins) whose preserved shell is also visible (marked J)
 - 4 Pelecypod *Sphenia anatina* (Basterot) adapted to the boring of *Gastrochaena* (cf. Radwański 1969, Pl. 35, Fig. 9); nat. size
 - 5 Pebble with pelecypods *Sphenia anatina* (Basterot) domiciled in diverse borings, mostly of *Lithophaga*; the largest shell is visible projecting out of the partly damaged boring (cf. Radwański 1969, Pl. 35, Fig. 10); nat. size
- 6 — Swarm of borings of the acrothoracican barnacles, *Zapfella pattei* Saint-Seine, within the abrasion surface bored by pelecypods (cf. Radwański 1969, Pl. 36, Fig. 2); Korytnica (locality marked Zp in Text-fig. 2); nat. size





Typical gastropods of the Korytnica Clays

1 — *Ancilla glandiformis* (Lamarck); 2 — *Murex friedbergi* Cossmann & Peyrot; 3 — *Tudicla rusticula* (Basterot); 4 — *Sigaretus striatus* de Serres; 5 — *Natica millepunctata* Lamarck; 6 — *Cypraea lanciae* Brusina; 7 — *Turritella badensis* Sacco; 8 — *Genota valeriae* (R. Hoernes & Auinger); 9 — *Conus ponderosus* Brocchi; 10 — *Aporrhais alatus* (Eichwald); 11 — *Pyrula geometra* Borson; 12 — *Fusus virgineus* sensu Hörnes, and sensu R. Hoernes & Auinger; 13 — *Triton nodiferum* Lamarck; 14 — *Terebra acuminata* Borson; 15 — *Ranella papillosa* Pusch, the shell contains a group of the slipper limpet *Crepidula crepidula* (Linnaeus): large female and two pygmy males, $\times 1.5$; 16 — *Clavatula laevigata* (Eichwald)

All figures in nat. size, except of Fig. 15

cerithids is regarded as indicative of restricted circulation, and the presence of mangroves (cf. Braithwaite & al. 1973, p. 311). The comparable gastropod communities of the present-day mangrove swamps are also reported from Madagascar, Mauritius, Mozambique and western Africa (cf. review and references in Plaziat 1970).

THE KORYTNICA CLAYS

During sedimentation in the Middle Miocene (Badenian) sea, the Korytnica Clays were covering almost the whole area of the basin (cf. Text-figs 2 and 4), although at present they are exposed on a rather strongly limited area (stippled in Text-fig. 2). In the remaining part of the basin, at the tops of morphologic elevations exposed now at the surface there are the members overlying the clays (marly sands and red-algal limestones; cf. Text-fig. 4), whereas in depressions used by streams of the present-day outflow, the Pleistocene glacial outwash sands and Recent black muddy soil make up the cover of the clays (cf. Text-fig. 2: blank are all the areas where the clays are not exposed at the surface).

The Korytnica Clays are of light yellow color, and they are well recognizable at the surface, especially when a deeper plowing was done. After rainfall, such places become whitish due to a great content of shell detritus, mostly of the small pelecypod *Corbula (Aloides) gibba* (Olivi). Larger gastropod shells are easily perceptible also in the soil over the whole cropland that features vast areas of the basin (cf. Text-fig. 3A—C: areas marked *gc*).

The Korytnica Clays are soft, plastic, and no bedding or any other physical sedimentary structures are discernible, except of local lamination caused by shell detritus. Due to the lack of any contrast between successive portions of the clays, neither burrows nor bioturbations are recognizable, although plenty of various endobenthic animals, i.a. gastropods and pelecypods (cf. Hoffman 1977), and some holothurians (cf. Walkiewicz 1977b) lived in the basin during deposition of the clays.

To begin with presenting the history of investigation of the Korytnica Clays, it should be noted that recently the occurrence of the fossils reworked from the substrate rocks has been indicated. It concerns the microfossils, both calcareous nannoplankton reworked from the Jurassic and Cretaceous deposits (Martini 1977), and some holothurian sclerites reworked from the Upper Cretaceous (Walkiewicz 1977b). If a delivery of the Jurassic fossils with the fine clastic material is quite obvious, as discussed above (chapter on the structure of the basin), the supply of the Cretaceous material has to prove a transport from the open sea areas, presumably through the strait in the place where at present the village Korytnica is situated (cf. Text-fig. 1C and 2).

HISTORY OF INVESTIGATION

The history of investigation of the Korytnica Clays has long been the history of recognition of their fossils (cf. Radwański 1969, Bałuk 1975), mostly gastropods, as this very group makes the most common and outstanding component of the organic world within the clays. These gastropod-bearing clays (cf. Text-fig. 3 and Pl. 2) have often been called the *Pleurotoma* Clays, as the pleurotomids, mostly of the genus *Clavatula* if not the commonest (cf. Pls 2—5), are certainly one of the most striking gastropods of the Korytnica Clays.

The locality of Korytnica was discovered presumably somewhere about the twenties of the last century (cf. Kowalewski 1930, Bałuk 1975), but the first description of its fossils appeared some twenty years later (Pusch 1837).

An international career of Korytnica began in the forties of the last century, when Sir R. I. Murchison on his famous way to Russia stopped in Poland specially to make a trip to this locality. His brief account on the locality and collected gastropods (Murchison 1845, pp. 292—293) completed that presented formerly by Pusch, and it was the first description of the regional situation of the clays.

The Korytnica gastropods were later included by Eichwald (1853), Hörnes (1856) and Hoernes & Auinger (1879) into their classical monographs of the Miocene malacofauna. The successively enlarging list of the mollusks was due to the works of Kontkiewicz (1882) and Kowalewski (1930), the latter of whom was also supplying the fossils to Professor W. Friedberg (1873—1941) who included them partly into his life paper „*Mollusca miocaenica Poloniae*”, published in seven parts (gastropods and scaphopods 1911—1928; pelecypods 1934—1936; guide to the collection 1938; for references to smaller contributions see Bałuk 1975; revision of the genus *Conus* — see Hall 1964). Both Dr. K. Kowalewski and Professor W. Friedberg were the first who paid attention to other fossils than mollusks, either publishing own contributions (cf. Friedberg 1924, 1930), or delivering the fossils to specialists in the country and abroad (e.g., polychaetes — Dembińska 1923; corals — Dembińska-Rózkowska 1932; fish otoliths — Chaine & Duvergier 1928). The scientific activity of Professor W. Friedberg and of Dr. K. Kowalewski closed the period preceding that of the recent investigators.

REVIEW OF THE ANIMAL GROUPS

The Korytnica Clays contain the fossils representing almost all the systematic groups of the animal kingdom (of vertebrates only fish are present) whose skeletal parts are recognizable in the ancient deposits. The state of their recognition and chances for further research are as follows.

Foraminifers

The abundant foraminifers have not hitherto been investigated systematically, except of the miliolids (Łuczowska 1974), and of some contributions on selected groups or genera (cf. Bałuk 1975; Walkiewicz 1975, 1977a).

Radiolarians

Infrequent radiolarians have not hitherto been studied systematically.

Sponges

The boring sponges are only recognized (cf. Radwański 1964, 1969, 1970; and this paper), as well as the presence of some others domiciled by cirripedes *Acasta* and/or by gastropods *Tenagodus* is inferred (cf. Bałuk & Radwański 1967, Bałuk 1975; and this paper).

Corals

The corals, both solitary and colonial, were recorded by most of the previous authors (cf. Bałuk 1975). They were included into the monograph of the Polish Miocene corals by Dembińska-Różkowska (1932). The genera *Flabellum* and *Acanthocyathus* were afterwards discussed by Kojumdgieva (1960), and/or by Kühn (1963) while the creusoid inhabitants in the species *Tarbellastraea reussiana* (Milne-Edwards & Haime) were studied by the authors (Bałuk & Radwański 1967; cf. also this paper). Recently, the corals are subjected to investigation by Dr. E. Roniewicz, Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

Polychaetes

The polychaetes are represented by boring forms (cf. Radwański 1964, 1969, 1970; and this paper), as well as by various tubular, either free-living (*Ditrupe*) or epizoic (*Spirorbis*, *Serpula*) forms (cf. Dembińska 1923, Bałuk 1975; and this paper).

Bryozoans

The bryozoans are recognized very imperfectly (cf. Bałuk 1975). The ecologically important genus *Cupuladria*, reported from here previously (Cook 1965, p. 199), is the subject of a separate paper by the authors (Bałuk & Radwański 1977). Special studies on the Korytnica bryozoans are recently kept by Professor J. Małecki, School of Mining and Metallurgy, Cracow.

Brachiopods

The previous reports on the brachiopods were very scant (cf. Friedberg 1930, Kowalewski 1930, Bałuk 1975). This group is now monographed by Barczyk & Popiel-Barczyk (1977).

Ostracodes

The ostracodes have not hitherto been systematically studied (cf. Bałuk 1975).

Crabs

The predatory activity of the hermit crabs upon the alive mollusks is a common feature of the Korytnica fossils (Radwański 1969, 1977b; cf. also this paper). A rich material of the claws, the only preserved parts of the crabs within the clays, is now investigated by Dr. R. Förster, University of Munich.

Cirripedes

A great assemblage of various cirripedes, containing representatives of common acorn barnacles and such genera as *Scalpellum*, *Conchoderma*, *Verruca*, *Chthamalus*, *Acasta*, *Creusia*, some of which have not hitherto been known from the Miocene (*Conchoderma*, *Chthamalus*), is the subject of the authors' own investigations. The first result, the paleontological and ecologic analysis of the *Creusia* species has been included into the monograph of the Miocene cirripedes domiciled in corals (Bałuk & Radwański 1967). Further investigations are in progress (cf. Radwański 1969, 1974a, b; Bałuk 1975; and this paper). The etching activity of the genus *Verruca* is presented separately (Radwański 1977b; cf. also Bałuk 1975, and this paper). The trace fossil species, *Zapfella pattei* Saint-Seine, attributed to the acrothoracican barnacles was recognized within the littoral ichnocoenoses of the basin (Radwański 1964, 1969, 1970; cf. also Bałuk 1975, and this paper).

Chitons

The assemblage of chitons, including fifteen species, and being therefore the richest in the European Miocene has been recently monographed by Bałuk (1971; cf. also this paper).

Scaphopods

The assemblage of scaphopods, including thirteen species, and being one of the richest in the European Miocene, has also been monographed by Bałuk (1972).

Gastropods

The most important component of the gastropod-bearing clays (cf. history of investigation) comprises an assemblage of about 800 species, some of which are new. This becomes the subject of a new monographing by Bałuk; the first volume has just recently appeared (Bałuk 1975), and the others are in preparation. Separately described by Bałuk & Jakubowski (1968) was the bivalved sacoglossan species of the genus *Berthelinia*, whose bearing on the facies conditions within the basin have been often reminded (Radwański 1969, 1974a, b, 1975; cf. also this paper). The predation by the muricids and naticids upon other mollusks, and their mutual competition in the finding and selecting of prey were studied by Hoffman & al. (1974), whereas mortality patterns of some species were described by Hoffman (1976b).

Pelecypods

The other important component of the clays comprises an assemblage of about 200 species, much richer than it was formerly recognized (cf. Kowalewski

1930; Friedberg 1931, 1932, 1934—1936, 1938). This assemblage is now investigated by Dr. G. Jakubowski, Museum of the Earth, Polish Academy of Sciences, Warsaw; he has recently included six Korytnica species into his monograph on the ontogenic development of some pelecypods from the Polish Miocene (Jakubowski 1972), and contributed on unique large pinnids from the marly sands overlying the clays (Jakubowski 1977). The rock-boring species, the same as secondary dwellers of empty borings were studied by Radwański (1964, 1965a, 1969, 1970, 1977b; cf. also this paper). Mortality patterns of some species have recently been presented by Hoffman (1976a).

Cephalopods

Of the cephalopods, only the presence of the cuttlefish has recently been recognized by Bałuk (1975), and subjected to paleontological description of a new species (Bałuk 1977).

Crinoids

The presence of the free-living comatulid crinoids of the genera *Antedon* and *Discometra* has recently been recognized by Bałuk (1975) who obtained them from siftings and now is finishing their description.

Holothurians

A very rich assemblage of the holothurian sclerites is recently monographed by Walkiewicz (1977b) who recognized eleven new species apart from some twenty common species. The presence of some other holothurians is inferred from the synecology of organic communities, and from some biologic relationships (see below).

Ophiuroids and starfish

Infrequent ossicles of both ophiuroids and starfish are collected (cf. Kowalewski 1930, Bałuk 1975) and they are ready for investigation.

Echinoids

The echinoids were very little known formerly (cf. Kowalewski 1930, Bałuk 1975), but now they became the subject of their monographing by Mażyńska (1977).

Fish

The fish otoliths are rather common material in the clays, and they have long been the subject of interest (Friedberg 1924, Chaine & Duvergier 1928, Śmigielńska 1966); their new monograph is prepared by Dr. T. Śmigielńska, School of Mining and Metallurgy, Cracow.

The tooth material, both of the elasmobranchs and teleosteans, previously reported very accidentally (cf. Kowalewski 1930, Bałuk 1975), and moreover some bone material of the teleosteans are now monographed by Schultz (1977).

ANIMAL COMMUNITIES

During sedimentation of particular horizons of the Korytnica Clays the bottom conditions, except of the littoral zone (see above), were almost uniform all over the basin (cf. Radwański 1969, Hoffman 1977). The same may be said when regarding the type of the bottom sediment that was laid down in the vertical succession of the clay member (see above). The fossil content in the vertical succession is however much differentiated, and it reflects the changes in organic (mostly mollusk dominated) communities which lived during the gradual filling of the basin by the clay deposits (cf. Radwański 1969; 1974a, b). The vertical succession of organic communities in any part of the clay sequence corresponds well to that established along the shore slope when the basin was formed (see idealized shorescape in Text-fig. 5, and succession of the communities in Text-fig. 6). The distribution of the fauna along the shore slope resulted then evidently from bathymetric requirements of particular genera or species, as follows.

The community of the deepest part of the shore slope (Community I in Text-fig. 5) is characterized by a solitary coral *Flabellum* (cf. Dembińska-Rózkowska 1932, Kojumdgieva 1960, Kühn 1963), large tusk shell *Dentalium* (*Antalis*) *badense* Partsch (cf. Bałuk 1972), and gastropods *Turritella* (cf. Bałuk 1975). This community is comparable to those typical at present of the depths ranging between 40 and 60 meters (cf. Radwański 1969).

The community of the middle part of the shore slope (Community II in Text-fig. 5) is characterized by the abundance of diverse gastropods, the most typical of which are various *Clavatula*, *Murex*, *Ancilla*, *Conus*, *Cypraea*, *Tudicla*, *Strombus* (schematically drawn in Text-fig. 5), as well as *Turritella*, *Cassis*, *Triton*, *Fusus*, *Chenopus*, various *Natica* and *Nassa* (cf. Pl. 2). Less common are *Ranella*, *Pyrula*, *Genota*, *Terebra*, and *Sigaretus* (cf. Pl. 2), as well as the slipper limpet *Crepidula crepidula* (Linnaeus) which inhabited empty shells of any other gastropods, and is often preserved in groups composed of a larger female and pygmy males perching on her (cf. Pl. 2, Fig. 15, and Pl. 3, Fig. 6). Associated are colonial corals, mostly *Tarbellastraea reussiana* (Milne-Edwards & Haime), and various pelecypods, whereas numerous incisions in shells show the remarkable role played by the hermit crabs (cf. Pls 10-12; discussion below). The rock-borers, the same as those occurring in the littoral zone (see below), appear in the shells within the discussed biotope (cf. Pls 3-5). There also appear the fragments of large-sized mollusks, mostly gastropods (cf. Pls 7-8) of the genera *Triton*, *Murex*, *Conus*, *Volutilithes*, *Cypraea*, *Cassis*, *Rostellaria*, *Strombus*, *Xenophora*, and *Galeodes*, whose presence makes a separate problem (see below). The whole Community II is comparable to those typical at present of the depths ranging between 20 and 40 meters (cf. Radwański 1969).

The community of the highest part of the shore slope (Community III in Text-fig. 5) is generally very similar to the preceding one, although many of the gastropods acquire larger size and thicker shells. Moreover, some new animals appear, the most attractive of which is the bivalved gastropod *Berthelinia* browsing on the kelp (the only locality of this gastropod in the European Miocene; cf. Pl. 9, Figs 1-3, and Bałuk & Jakubowski 1968), various chitons with *Craspedochiton* and worm-shaped *Cryptoplax* (cf. Pl. 9, Figs 6-7; and Bałuk 1971),

cirripedes *Creusia* domiciled in corals (cf. Pl. 9, Fig. 8; and Bałuk & Radwański 1967), as well as *Verruca*, *Chthamalus* and common acorn barnacles *Balanus*. The discussed genera live today along rocky coasts or in coral reefs just below low water level (some of them even spreading up into the intertidal zone). The whole Community III is therefore regarded as living at the depths shallowing from some twenty to a few meters (cf. references in Bałuk 1971, Bałuk & Jakubowski 1968, Bałuk & Radwański 1967, Radwański 1969).

✓ The whole sequence of the Korytnica Clays, as shown by the above characteristics of the organic communities and their life conditions, should consequently be interpreted as formed in the successively shallowing basin. Due to gradual storage of the clay deposit, the depth of the basin was successively decreasing, and the organic communities, previously distributed laterally at various depth ranges of the shore slope (cf. Text-fig. 5) could spread over the whole basin to repeat vertically their former lateral array (cf. Text-fig. 6). The original depth of the basin was of that value to which the pre-Miocene valley (cf. Text-fig. 1C) was drowned during the transgression, whereas the final portion of the clays was deposited at the extreme shallow depths, but still within the submerged zones (cf. Text-fig. 6 and see below: chapter on seagrass vegetation).

SEAGRASS VEGETATION

The analysis of the whole animal assemblage of the Korytnica Clays shows that the presence of the seagrass meadows must be taken into account when considering the synecologic relationships. This is apparent both from the composition of particular communities which are well comparable to those confined to seagrasses in present-day environments (Hoffman 1977), especially of the Indian Ocean (cf. Taylor 1971), and from the indistinct etchings on the mollusk shells, which are regarded as counterparts of those left by seagrass roots in the present-day habitats (cf. Hoffman 1977, Cottrell 1977, Radwański 1977b).

Additional argumentation is delivered by a common presence, in some habitats at least, of the animals which in present-day environments live primarily within the seagrass spots. This is true for such groups, or particular genera and species, as: cuttlefish (cf. Bałuk 1977; and Starmühlner 1963b); free-living comatulid crinoids of the *Antedon* type (cf. Strenger 1963a); some holothurians (cf. Walkiewicz 1977b; and Strenger 1963b); echinoids *Echinocyamus* which have recently been recorded from the clays (Bałuk 1975, Maćzyńska 1977) and which are mostly confined to such habitats (cf. Szörényi 1953, Strenger 1963c). Similar conclusion is also drawn from the presence of the foraminifer species

Amphistegina lessonii d'Orbigny which lived through the almost whole time of deposition of the clays (cf. Walkiewicz 1975; and Bandy 1964, Rosenkrands Larsen 1976).

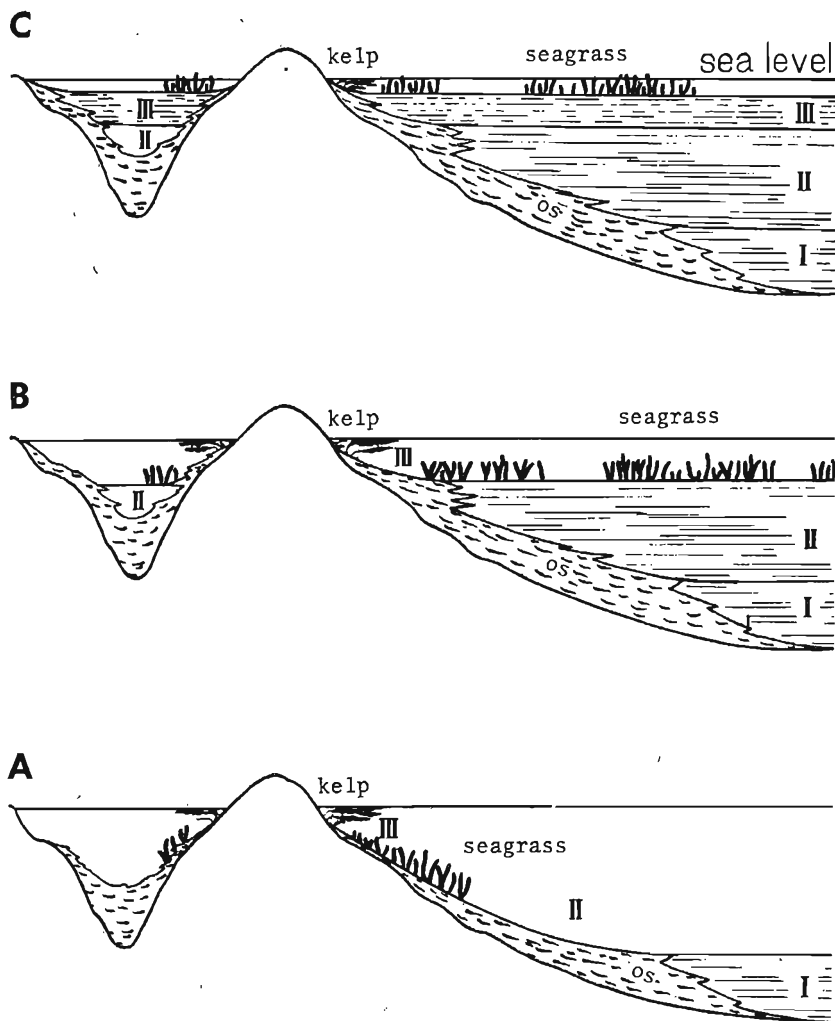


Fig. 6. Succession of the organic communities (I, II, III) during the formation of the Korytnica Clays (cf. Text-fig. 5)

A — Time after deposition of the lowermost part of the Korytnica Clays (characterized by the community I) and a contemporaneous part of the oyster shellbed (os); communities II and III spread over higher parts of the submerged slope, the same as the seagrass and kelp

B — Time after deposition of the middle part of the Korytnica Clays (characterized by the community II) and a contemporaneous part of the oyster shellbed (os); community III spreads over higher parts of the submerged slope; the seagrass meadows cover the bottom almost entirely

C — Time during deposition of the uppermost part of the Korytnica Clays (characterized by the community III) and a contemporaneous part of the oyster shellbed (os); the seagrass meadows still cover the bottom almost entirely, and locally stretch out of the sea level

The seagrass communities during deposition of the lowest part of the Korytnica Clays were thriving mostly along the submerged slopes of the seashore where the photic requirements were sufficient for their vegetation (cf. Text-fig. 6A). The seashore slopes were then occasionally covered by seagrasses, whereas in the remaining areas either rocky substrate was stretching out of the sediment surface, or the oyster shellbed was formed. Later, when the basin was successively shallowing, the seagrass communities were spreading throughout the basin (cf. Text-fig. 6B), and such a situation lasted until the uppermost part of the clays was deposited. At that time the seagrass meadows could reach sea level in some places (cf. Text-fig. 6C), in a way similar to that at the tops of mud banks on the Florida offshores (cf. Ginsburg & Lowenstam 1958). The same situation is also recognizable for the time of deposition of the marly sands that overlie the Korytnica Clays (cf. Radwański 1977a).

FOSSILS OF THE KORYTZNICA CLAYS

In this chapter presented are such new data on the distribution, ecology, taphonomy, and state of preservation of the fossils from the Korytnica Clays, which have a bearing upon general conclusions on the life and preservation conditions within the Korytnica basin.

DISTRIBUTION

All the fossils within the Korytnica Clays are distributed very ununiformly. As it is apparent in trenches, the fossils are often concentrated in streaks or thin lenses in which the frequency of particular species much varies. Larger gastropods are to be found sometimes in groups on small areas, whereas in other places they occur very sporadically and are dispersed singly in the clay.

The abundance of gastropods within all the successive horizons of the Korytnica Clays is certainly remarkable, as they are often represented by numerous specimens of a few species of the same genus (e.g. *Clavatulula*, *Natica*, *Nassa*). Either these species were of different ecological requirements within the same biotope, or the shell accumulation in the deposit came from various biotopes of lateral and/or vertical succession. It seems that generally the necrocoenoses correspond to life habitats of the gastropods, as no significant post-mortem sorting or transportation is indicated (cf. Hoffman 1977). Nevertheless, it is difficult to recognize which species lived quite contemporaneously, as the particular necrotopes contain the species not only epibenthic, but also (e.g. *Natica*) endobenthic. On the other hand, a local segregation

and transportation of shells became an important factor, especially outside the seagrass meadows. Finally, when regarding the shell distribution, such biological agents of transportation should be taken into account as the activity of scavengers, and of the hermit crabs using the shells as their homes.

TAPHONOMY

The burial conditions during sedimentation of the Korytnica Clays were much differentiated and, if no significant transportation of the shells is kept in mind, they should be ascribed mostly to a variable sedimentation ratio.

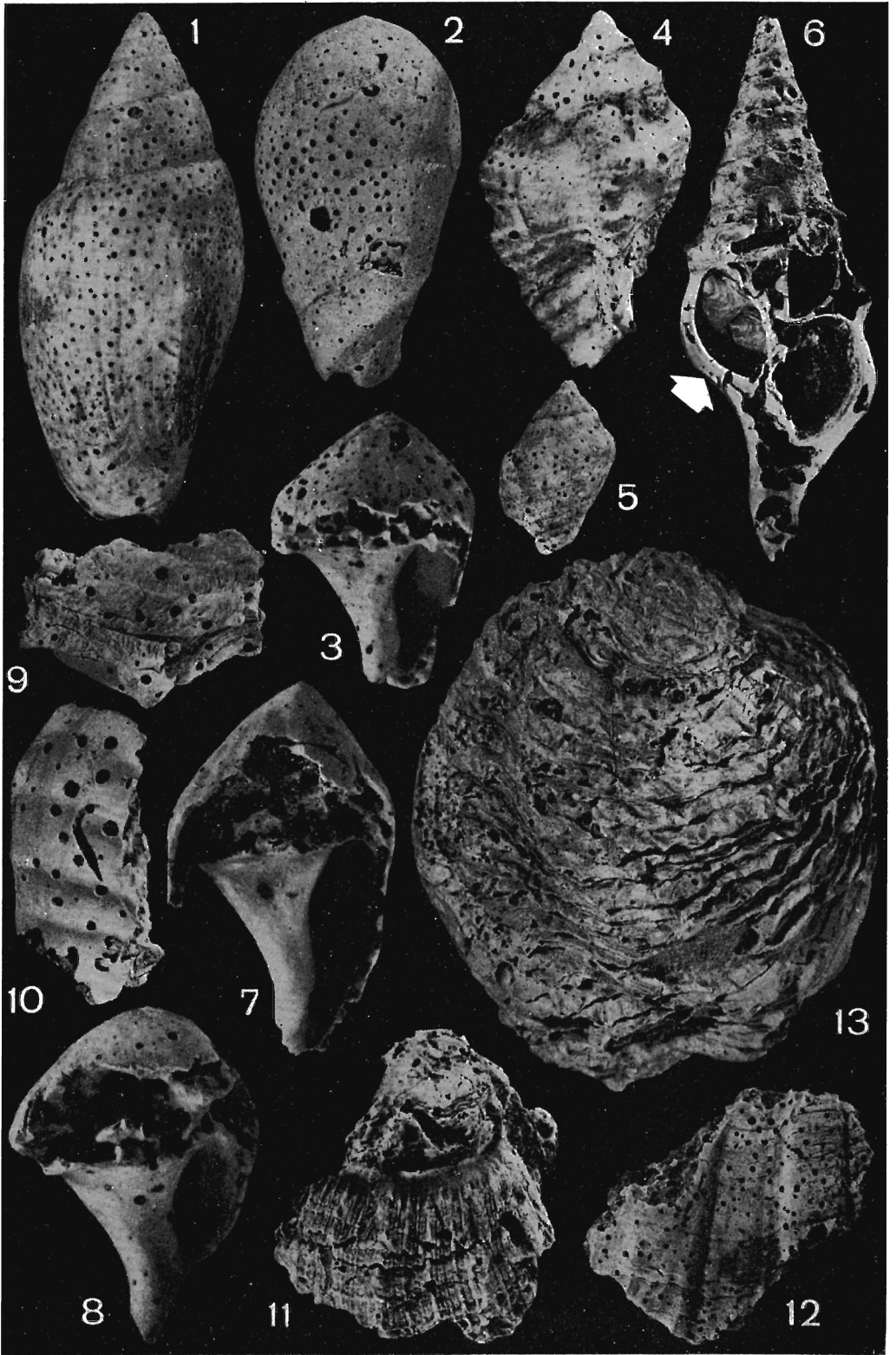
Most of the shells contained in the Korytnica Clays are fresh, and these were supposedly buried just after the death of the host. There are however commonly met various shells more or less corroded, or strongly damaged due to the organic activity. The corrosion is expressed by a frosty surface, usually of one side that was stretching over the sea floor. Some shells are bored by rock-borers in the same way, similarly as those encrusted by the epizoans (*see below*). It is therefore apparent that such shells were partly buried to a definite level, presumably quickly, and afterwards they were stretching naked with their upper parts out of the sea floor for a longer span of time. Such shells became then the sedimentary traps for small-sized fossils which concentrated here in comparison with the clay adjacent to the entrapping shell, and which met here exceptional conditions for their preservation. This is well demonstrated for juvenile pelecypods (cf. Jakubowski 1972) and brachiopods (cf. Barczyk & Popiel-Barczyk 1977), chitons (cf. Bałuk 1971), some tiny gastropods (cf. Bałuk 1975), and for free-living bryozoans (cf. Bałuk & Radwański 1977).

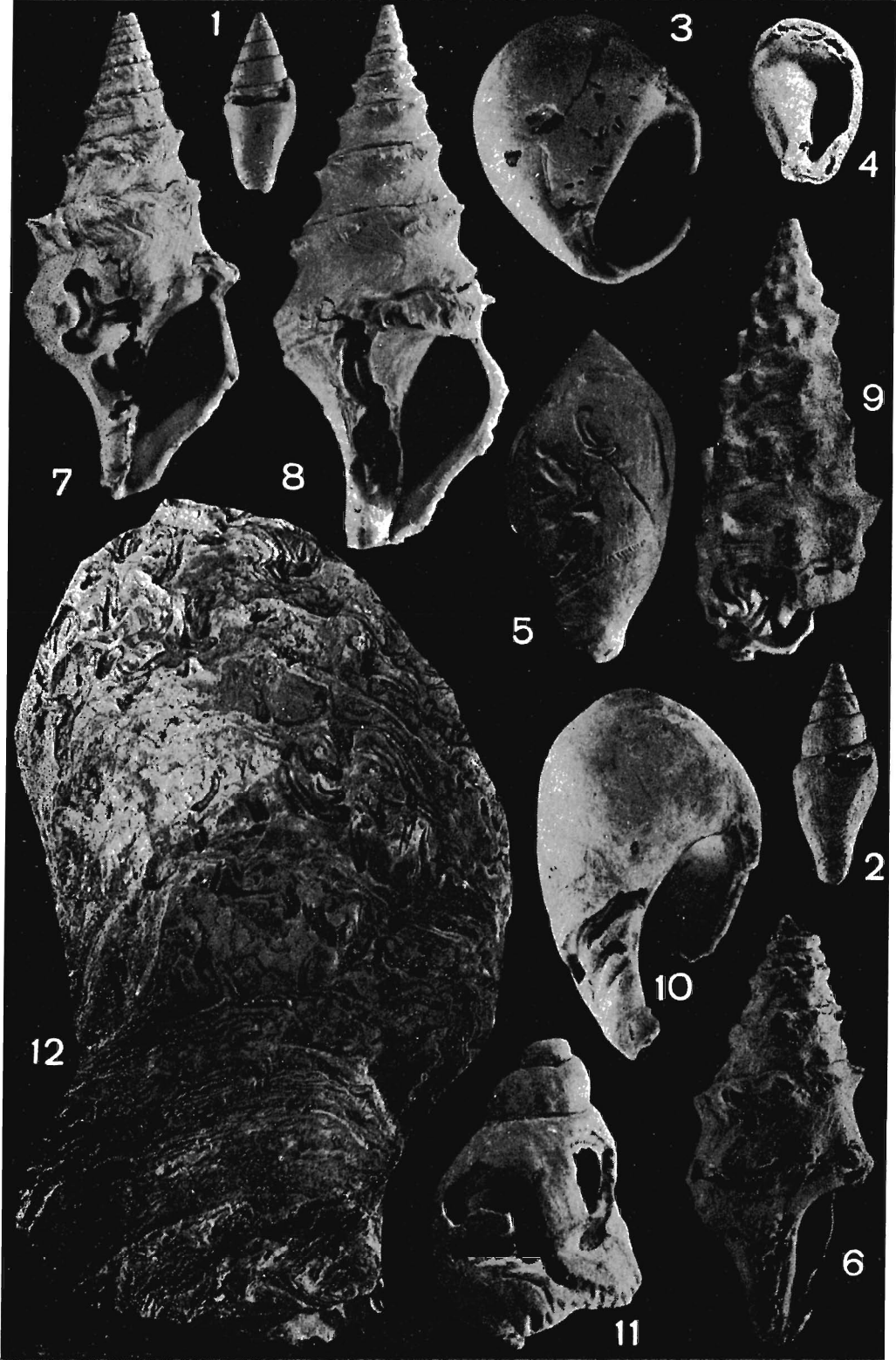
On the other hand, the preservation of some gastropod shells inhabited by the slipper limpet *Crepidula crepidula* (Linnaeus), the female of which often carries one or a few pygmy males on her shell

PLATE 3

Activity of boring sponges in the mollusk shells of the Korytnica Clays

- 1—5 — Borings of *Cliona vastifica* Hancock in the gastropod shells: 1 — *Lyria taurinia* (Bonelli), 2—3 — *Ancilla glandiformis* (Lamarck), 4 — *Ocenebra erinacea* (Linnaeus), 5 — *Purpura exilis* Partsch; all $\times 1.5$
- 6—10 — Borings of *Cliona celata* Grant in the gastropod shells or their fragments: 6 — *Clavatula asperulata* (Lamarck) — the shell is partly cut-off to show the slipper limpet *Crepidula crepidula* (Linnaeus) settled inside (arrowed): large female with a pygmy male; 7—8 — *Ancilla glandiformis* (Lamarck), 9 — fragment of *Xenophora deshayesi* (Michelotti), 10 — fragment of *Triton nodiferum* Lamarck; all $\times 1.5$
- 11—13 — Clionid borings in the pelecypod shells or their fragments: 11 — fragment of *Spondylus crassicosta* Lamarck, and 12 — fragment of *Chlamys latissima nodosiformis* (de Serres), both bored by *Cliona celata* Grant; 13 — *Chama gryphoides garmella* de Gregorio bored by *Cliona vastifica* Hancock; all in nat. size





(cf. Fig. 15 in Pl. 2, and Fig. 6 in Pl. 3), evidences no transportation, and a rapid burial.

It may therefore be concluded that the shells contained in the Korytnica Clays were lying on the sea floor for a various span of time: some were buried very quickly, while some others underwent a gradual destruction (*see below*). The latter ones could certainly then became the components of such necrocoenoses to which new shells were temporarily delivered.

Recently it is suggested (Bałuk 1977) that of the nectic cuttlefish, preserved in the clays were the skeletal parts of only these individuals which, during their seasonal migration to the Korytnica basin (*see below*), had become the prey of the predators.

It may be also noted that the burial conditions during sedimentation of the Korytnica Clays were favorable for preservation of color pattern in some fossils. This is well recognizable in some gastropods (cf. Bałuk 1975), the bivalved *Berthelinia* including (cf. Pl. 9, Fig. 3a; and Bałuk & Jakubowski 1968), as well as in the creusoid barnacles (cf. Pl. 9, Fig. 8; and Bałuk & Radwański 1967).

ENDO- AND EPIZOANS

The shells of the fossils contained in the Korytnica Clays often became the habitat of various endo- and epizoans, the activity of which was either pronounced on one side of the shell (as indicated above), or on its whole (cf. Pls 3—6).

The endozoans are represented generally by the same rock-borers which are present in littoral rubbles and abrasion surfaces (cf. Text-fig. 5), except of the acrothoracian barnacles (cf. Radwański 1969, 1970). Their damage in the mollusk shells is either local, or very total and resulting in their fragmentation into pieces.

PLATE 4

Activity of boring polychaetes in the mollusk shells of the Korytnica basin

- 1—5 — Borings of *Polydora ciliata* (Johnston) in the gastropod shells from the Korytnica Clays: 1—2 — *Columbella curta* (Dujardin) — the borings exposed to show their position paralleling the adapical channel of the last whorl; 3 — *Natica redempta* Michelotti — vertical borings in the callus; 4 — *Ancilla glandiformis* (Lamarck) — borings extended around the aperture; 5 — another *Ancilla glandiformis* — shallow borings on the outer surface of the shell; all $\times 1.5$
- 6—11 — Borings of *Polydora hoplura* (Claparède) in the gastropod shells from the Korytnica Clays: 6 — *Clavatula laevigata* (Eichwald) — openings of numerous borings are visible; 7 — *Clavatula asperulata* (Lamarck), and 8 — *C. laevigata* — the borings exposed to show their position within the columella and the last whorl; 9 — *Cerithium vulgatum miospinosum* Sacco — a group of borings exposed, 10 — *Ancilla glandiformis*, and 11 — fragment of *Euthria puschi* (Andrzejowski) — in both the borings are exposed; all $\times 1.5$
- 12 — Numerous borings of *Polydora hoplura* (Claparède) in the oyster, *Crassostrea gryphoides* (Schlotheim), from the marly sands at Chomentów (cf. Radwański 1969, Pl. 41, Fig. 1); nat. size

The boring sponges, *Cliona celata* Grant and *C. vastifica* Hancock, lived in gastropod and pelecypod shells (Pl. 3, Figs 1—13), resulting often in their total damage (cf. Pl. 3, Figs 3 and 7—12). Some small fragments, strongly bored by sponges (cf. Pl. 3, Figs 9—12) certainly come from the shells heavily destroyed which have therefore easily been broken into pieces.

The boring polychaetes, *Polydora ciliata* (Johnston) and *P. hoplura* (Claparède), settled mostly in the gastropod shells (Pl. 4, Figs 1—11), while in the pelecypod shells this second species is common, but it occurs mostly in the marly sands overlying the clays (Pl. 4, Fig. 12). These two polychaetes were boring at various depth and at various angle to the shell surface (cf. Pl. 4, Figs 5—10), some of the borings having been slightly incised into the shell (Pl. 4, Fig. 5). Larger borings, those of *P. hoplura*, are often situated along the thickest part of the shell, e.g. along the columella (Pl. 4, Fig. 8). In smaller borings, those of *P. ciliata*, it is not so common, although in the shells having the callus, this part is bored primarily (Pl. 4, Fig. 3). Some borings of *P. ciliata* are situated along the aperture of the shell (Pl. 4, Fig. 4) which may evidence their origin during the gastropod life. This latter possibility should mostly be taken into account in the species *Columbella curta* (Dujardin), the shells of which contain often only one boring of *P. ciliata*, but it continues along the adapical channel (Pl. 4, Figs 1—2).

Of the pelecypods boring in the littoral zone of the basin, only *Gastrochaena dubia* (Pennant) is present in the mollusk shells of the Korytnica Clays (cf. Pl. 3, Figs 1—9). Sporadically, borings of *Petricola* sp. may also be found in the clays (Radwański 1969). The gastrochaenid borings are well attributable to the species indicated above, *G. dubia* (Pennant), as their shells are often preserved in the borings (cf. Pl. 5, Fig. 8b). Many of these borings were only partly embedded in the shell, and their upper parts were covered by an agglutinaceous tube; when the latter have been removed, the "half borings" appeared from beneath (cf. Pl. 5, Figs 2 and 4—5). Agglutinaceous is also the siphonal collar that outlined the siphons stretching out of the shell surface (cf. Pl. 5, Figs 1—2), the same as out the rock surface in the littoral zone (cf. Pl. 5, Fig. 3). The mode of formation of the agglutinaceous parts of the tube that may complete the partial borings is the same as in present-day gastrochaenids, the species *G. dubia* (Pennant) including (cf. references in Radwański 1969; also Wärme 1975, Fig. 11.25). The frequency of the gastrochaenid borings on one shell varies from a single

PLATE 5

Activity of boring pelecypods, *Gastrochaena dubia* (Pennant), at the rocky seashore, and in the mollusk shells of the Korytnica Clays

1—2 — Borings of *Gastrochaena dubia* (Pennant) provided with the agglutinaceous siphonal collar that stretches out of the shells of *Ancilla glandiformis* (Lamarck); in 2, upper part of the boring wall has not been preserved (this is the "half boring"); $\times 1.5$

3 — Agglutinaceous siphonal collar stretching out of the rocky surface; an epizoic coral is visible nearby (cf. Radwański 1969, Pl. 34, Fig. 3; 1970, Pl. 3b); $\times 2$

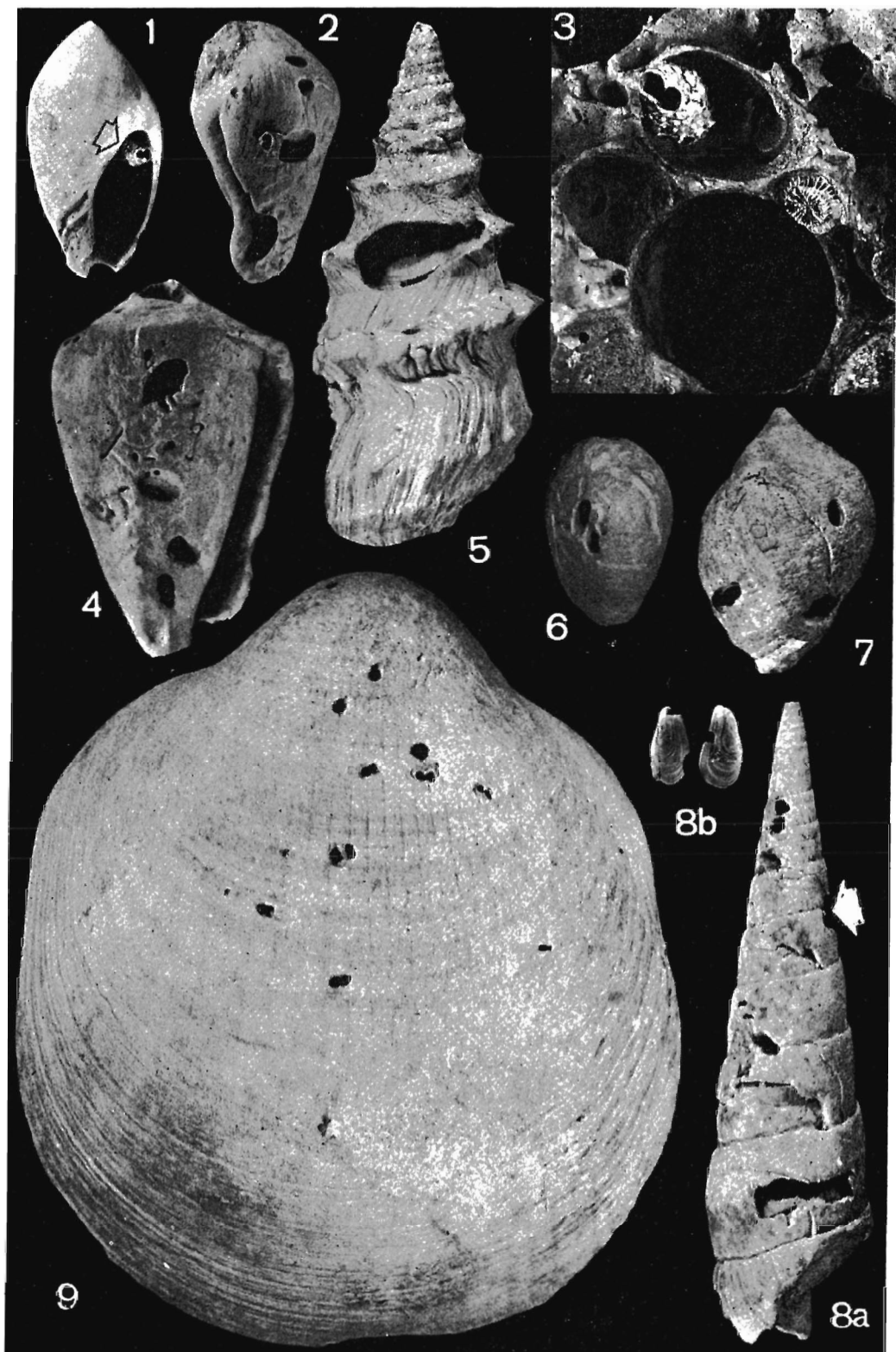
4 — Numerous "half-borings" in *Conus* sp.; $\times 1.5$

5 — "Half-boring" oriented tangentially in *Clavatula asperulata* (Lamarck); $\times 1.5$

6—7 — "Half-borings" oriented vertically in: 6 — *Cypraea lanciae* Brusina, 7 — *Purpura exilis* Partsch; $\times 1.5$

8a — *Terebra fuscata* (Brocchi) with a few borings, in one of which (arrowed) was preserved the shell of *Gastrochaena dubia* (Pennant) presented in 8b; both $\times 1.5$

9 — Vertically oriented borings in *Glycymeris pilosa deshayesi* (Mayer); nat. size





occurrence (cf. Pl. 5, Fig. 1) to several specimens (cf. Pl. 5, Figs 4 and 6—8) and larger groups of the borings, especially within the larger shells of pelecypods (cf. Pl. 5, Fig. 9).

A general conclusion as to the endozoans in the mollusk shells of the Korytnica Clays is that they occur in all the horizons of the clays, and therefore the depth of the basin was convenient for settlement of the littoral rock-borers through the whole time of clay deposition. The rock-borers which inhabited the shore slope during the transgression (cf. Text-fig. 5) were always able to settle in any hard objects, i.e. the mollusk shells when they appeared in the areas of clay sedimentation. Within the mollusk shells there is no preference to any rock-borers, and almost all the recognized species have been infested to some extent. An average value of the shells infested in particular species is however low, and it may be estimated as about 3—5%.

The activity of the epizoans within the mollusk shells of the Korytnica Clays, the oyster shellbed including, is recognizable by the presence of etchings (cf. Radwański 1977b) produced by the cirripedes of the genus *Verruca* when their shells were attached (Pl. 6, Fig. 3a—3b; cf. Radwański 1974b, 1977b). The other, deep etchings which may also be regarded as borings (Pl. 6, Fig. 4), belong to the bryozoan genus *Spathipora*, the systematic studies on which are now kept by the authors. Indistinct etchings left by seagrass roots (see above) complete the list of the hitherto recognized taxa.

Some epizoans are preserved with their hard parts, as it is exemplified by tubes of *Spirorbis* sp.¹ (Pl. 6, Figs 1—2) and other

¹ Specific determination of these spirorbids is not obvious at the moment. Previously reported from the Korytnica Clays was only *Spirorbis obtectus* Seguenza, listed by Kowalewski (1930, p. 71 and 111) who incorrectly suggested its biological relationship to the gastropod *Ancilla glandiformis* Lamarck, on the shells of which it was found. This spirorbid species was included by Rovereto into the synonymy of *Spirorbis (Laeospira) umbiliciformis* (Münster), but such an assignation has not been accepted by Schmidt (1955). The investigated specimens are partly comparable to those of the latter species, and presented by Schmidt (1955; Pl. 8, Fig. 32).

PLATE 6

Activity of encrusting and etching invertebrates in the mollusk shells of the Korytnica Clays

1 — Polychaetes *Spirorbis* sp. and a bryozoan encrusting *Lyria taurinia* (Bonelli); encrusted is the apertural side of the shell bored by clionid sponges (its opposite side being presented in Pl. 3, Fig. 1); × 1.5

2 — Group of polychaetes *Spirorbis* sp. encrusting the inner side of the shell of *Tudicla rusticula* (Basterot); × 5

3a — Shell of the gastropod *Lemintina arenaria* (Linnaeus) from the oyster shellbed (the specimen presented by Baluk 1975, Pl. 14, Fig. 14) encrusted by an oyster (*Oy*) end etched by verrucid barnacles, *Verruca* sp.

the most etched part (arrowed) is magnified in 3b; nat. size

3b — Part of the shell presented in the preceding photo, to show the pit-shaped etchings produced by *Verruca* sp. (cf. Radwański 1977b, Pl. 8c); × 5

4 — Deep etchings produced by bryozoans *Spathipora* sp. in the shell of *Ancilla glandiformis* (Lamarck); × 5

polychaetes, as well as by very uncommon bryozoan colonies (Pl. 6, Fig. 1) and corals, the latter being also known from the littoral zone (cf. Pl. 5, Fig. 3). Within the oyster shellbed with *Ostrea frondosa* de Serres, many shells are encrusted by this very oyster (cf. Pl. 6, Fig. 3a).

OCCURRENCE AND PRESERVATION OF LARGE MOLLUSKS

The presence of very large-sized mollusks, mostly gastropods, is a very characteristic feature of the middle and upper part of the Korytnica Clays (cf. Radwański 1969, p. 103; 1974a, p. 112). In these members of the clays, i.e. within the communities II and III (cf. Text-fig. 5) such gastropod shells are enough commonly found, but all are preserved in fragments (cf. Pls 7—8). Some of them are strongly damaged by rock-borers (e.g., Pl. 7, Fig. 7b; Pl. 8, Figs 1 and 3a), the same as those occurring both in the littoral zone and in "normal"-sized shells (cf. Pls 1 and 3—4), but others are quite fresh. Most of the fragmented large gastropods bear remarkably thick shells, and their so severe damage is therefore puzzling.

Of the hitherto recognized gastropod species, all here discussed are much larger than the undamaged specimens of these species from the Korytnica Clays, and some of them are even larger than the largest ones from the other European localities (mostly of the Paratethys basin — cf. Text-fig. 1A), as follows:

Triton nodiferum Lamarck — the collected specimens (Pl. 7, Fig. 1) belonged to individuals attaining c 185—190 mm in their height, being larger than those from the Vienna Basin (cf. Hörnes 1856). Similar larger forms are however known from the Pliocene of Italy and Cyprus. A mould of the specimen of comparable size (c 170 mm) was formerly reported also from the marly sands that overlie the Korytnica Clays (Radwański 1969, p. 106).

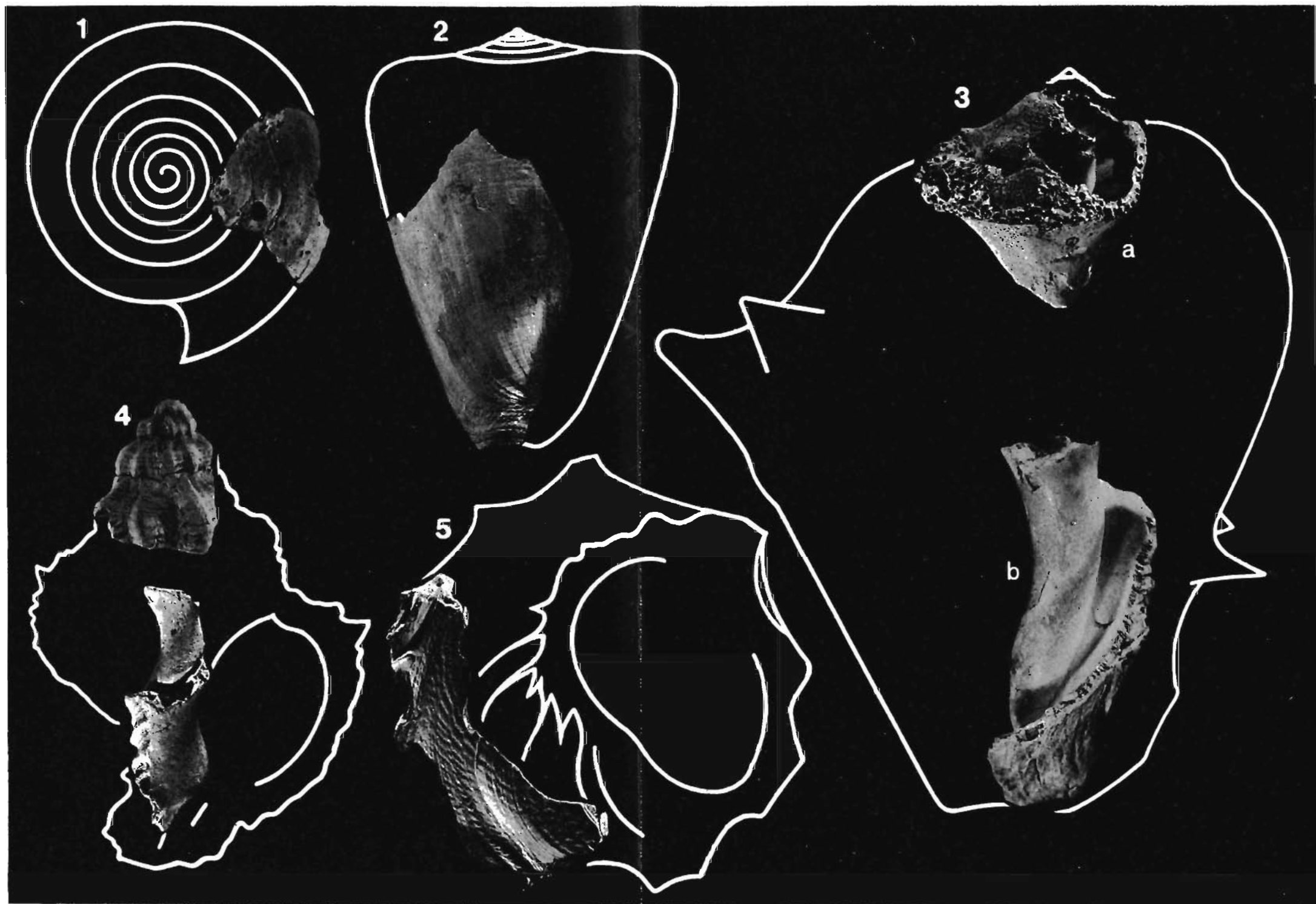
Cassis miolaevigata Sacco — the collected specimen (Pl. 7, Fig. 2) was c 65 mm high, being therefore of the size comparable to that of the Vienna specimens (cf. Hörnes 1856).

Volutilithes haueri (Hörnes) — the collected specimen (Pl. 7, Fig. 3) was c 70—75 mm high, being much larger than those from the Vienna Basin (cf. Hörnes 1856, Hoernes & Auinger 1879), Hungary (cf. Strausz 1966), and Bulgaria (cf. Kojumdgieva 1960).

Cassis cypraeiformis Borson — the collected specimen (Pl. 7, Fig. 4) was c 80 mm high, being also much larger than those from the Vienna Basin (cf. Hörnes 1856, Hoernes & Auinger 1879) and Hungary (cf. Strausz 1966).

Rostellaria dentata Grateloup — the collected specimens (Pl. 7, Fig. 5 a, b) belonged to individuals attaining c 180 mm in their height, being therefore of the size comparable to that only known in specimens from Baden in the Vienna Basin (cf. Hörnes 1856).

Strombus coronatus sensu R. Hoernes & Auinger — the collected specimens (Pl. 7, Fig. 6) belonged to individuals attaining c 100 mm in their height, being of the size almost identical with that in specimens from the Vienna Basin (cf. Hörnes 1856), and from Lapugy in Transylvania (cf. Hoernes & Auinger 1879).



Fragments of the shells of large gastropods from the Korytnica Clays (cf. explanation to Pl. 7; the reverse side of this fold-out); nat. size
 1-2 — Diverse *Conus* sp. 3 — *Galeodes cornutus* (Agassiz), 4 — *Murex austriacus* Tournouër, 5 — *Xenophora deshayesi* (Michelotti)



Fragments of the shells of large gastropods from the Korytnica Clays; the hypothetical outline of the shell is shown as taken from the comparative material (some fragments do not match exactly these outlines, being derived from the specimens of morphological ratios others than that one used to draw the outline); nat. size
 1 — *Triton nodiferum* Lamarck, 2 — *Cassis miolaevigata* Sacco, 3 — *Volutilithes haueri* (Hörnes), 4 — *Cassis cypraeiformis* Borson, 5 — *Rostellaria dentata* Gratcloup, 6 — *Strombus coronatus* sensu R. Hoernes & Auinger, 7 — *Cypraea* sp.

Cypraea sp. — the collected specimen (Pl. 7, Fig. 7) was c 70 mm high, which however does not reach the size of various large cowries from the Vienna Basin (cf. Hörnes 1856, Hoernes & Auinger 1879).

Diverse *Conus* sp. — the collected specimens (Pl. 8, Figs 1—2) certainly belonged to different species; a fragment of the spire (Pl. 8, Fig. 1) is not evidently determinable, whereas a fragment of the last whorl (Pl. 8, Fig. 2) presumably belonged to *Conus daciae* Hoernes & Auinger, being of the size (c 90 mm) comparable to that reported by Hoernes & Auinger (1879) from the Vienna Basin and Lapugy in Transylvania.

Galeodes cornutus (Agassiz) — the collected specimens (Pl. 8, Fig. 3 a, b) belonged to individuals attaining c 160 mm in their height, being therefore the largest bulbous, thick-shelled, and thus the "heaviest" gastropods of the Korytnica basin, although they were much smaller than those from Niederkreuzstätten in the Vienna Basin (205 mm high; cf. Hörnes 1856), and from the world-famous collection site of this species at Varpalota in Hungary (c 220 mm high; cf. Strausz 1966).

Murex austriacus Tournouër — the collected specimens (Pl. 8, Fig. 4) belonged to individuals attaining c 100 mm in their height, being therefore a little larger than those from Enzesfeld in the Vienna Basin (cf. Hoernes & Auinger 1879).

Xenophora deshayesi (Michelotti) — the illustrated specimen (Pl. 8, Fig. 5), and many other fragments of similar size, belonged to individuals attaining even c 100 mm in their width (e.g., the specimen in Pl. 8, Fig. 5, the outline of which is drawn smaller than it should be taken from that fragment — comp. the lowest part of the photo). Such specimens were evidently wider than the widest ones from the Vienna Basin (cf. Hörnes 1856); although they were of the size of those from Hungary (cf. Strausz 1966).

The two of the above listed species, *Volutilithes haueri* (Hörnes) and *Galeodes cornutus* (Agassiz), are hitherto known from the Korytnica Clays only from such damaged fragments.

It was previously suggested (Radwański 1969, p. 103; 1974a, p. 112) that the discussed large gastropods presumably lived within the littoral rubble where they underwent damage by grinding between stones in the surf zone, and then the fragments were swept away the shore. This may explain why the two above-mentioned species are unknown from the offshore facies, but it cannot clarify why some fresh-looking fragments are found in areas distant to the shore, wherefrom no evident transport is indicated (cf. Hoffman 1977). It seems therefore that even the species with the thickest shells lived far away the shore. If so, the only assumed cause of their total damage is the activity of predators, supposedly of that kind as huge crabs, or large vertebrates such as some fish or mammals².

The large-sized pelecypods from the Korytnica Clays certainly underwent similar damages as the gastropods did, although they occur

² In this respect, even the presence of terrestrial or semi-aquatic mammals may also be taken into account, as indicated by a commonly referenced example of the Californian sea otter which, when dived up the shell, floats on his back nearshore and hammers this shell against the stone he carries on his stomach! (cf. Bishop 1975, p. 265).

very sporadically and never make an essential content of the necrocoenose. They are represented by a few species only, such as: *Glycymeris pilosa deshayesi* (Mayer) whose isolated valves are often bored by *Gastrochaena* sp. (cf. Pl. 5, Fig. 9); *Cardium hians danubianum* Mayer and *Meretrix gigas* (Lamarck) preserved in small fragments; *Chama gryphoides garmella* de Gregorio whose isolated valves are damaged by clionid sponges (cf. Pl. 3, Fig. 13), the same as small fragments (cf. Pl. 3, Figs 11—12) of *Spondylus crassicosta* Lamarck and *Chlamys latissima nodosiformis* (de Serres), the latter species of which has not hitherto been reported from the Korytnica Clays.

BIOLOGIC RELATIONSHIPS

Some biological relationships which persisted in the basin during deposition of the Korytnica Clays are well demonstrated by natural associations which have been preserved in their life relation. This is shown the best by the creusioid barnacles, *Creusia sanctacrucensis* Bałuk & Radwański which lived, as commensals, within alive colonies of the corals *Tarbellastraea reussiana* (Milne-Edwards & Haime) that occur in the middle and upper part of the clays (cf. Pl. 9, Fig. 8; and Bałuk & Radwański 1967).

Other examples of similar relationships are inferred from the presence of one species, the partner of which remained however unpreserved. This is well demonstrated e.g. by the cirripedes *Acasta* which have been stated in the oyster shellbed (cf. Bałuk & Radwański 1967, p. 498), and which in present-day environments are exclusively adapted to live embedded in the sponges (cf. Darwin 1854). The same partner, a sponge, is inferred from the presence (cf. Pl. 9, Fig. 4) of

PLATE 9

Some ecologically important (commensal or thermophilic) invertebrates from the uppermost part of the Korytnica Clays

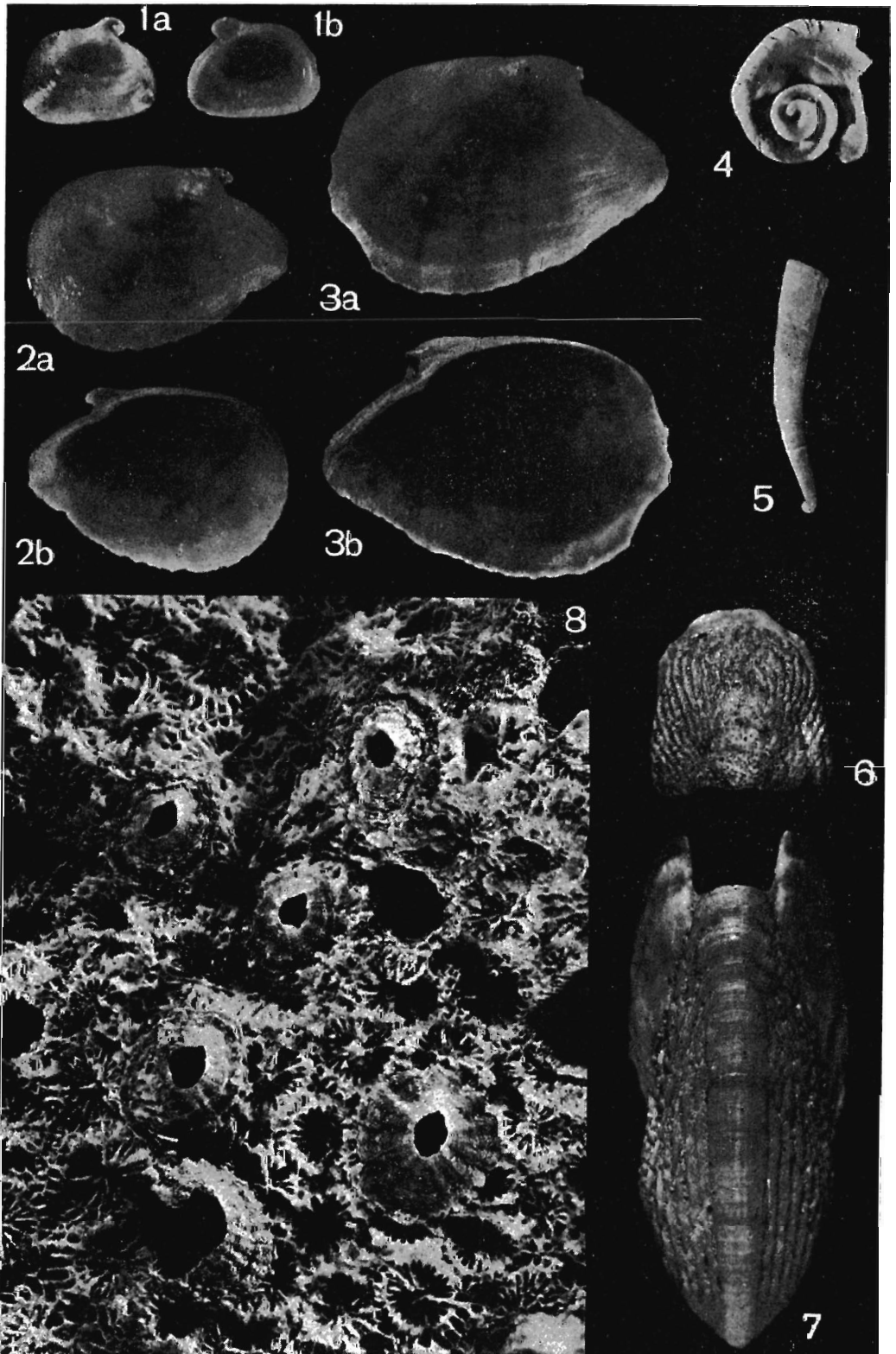
1—3 — Bivalved gastropods, *Berthelinia krachi* Bałuk & Jakubowski; well discernible color pattern displayed by radial stripes visible in 3a; left valves, to show the protoconch — a outer, b inner view (cf. Bałuk & Jakubowski 1968, Pl. 1); × 20

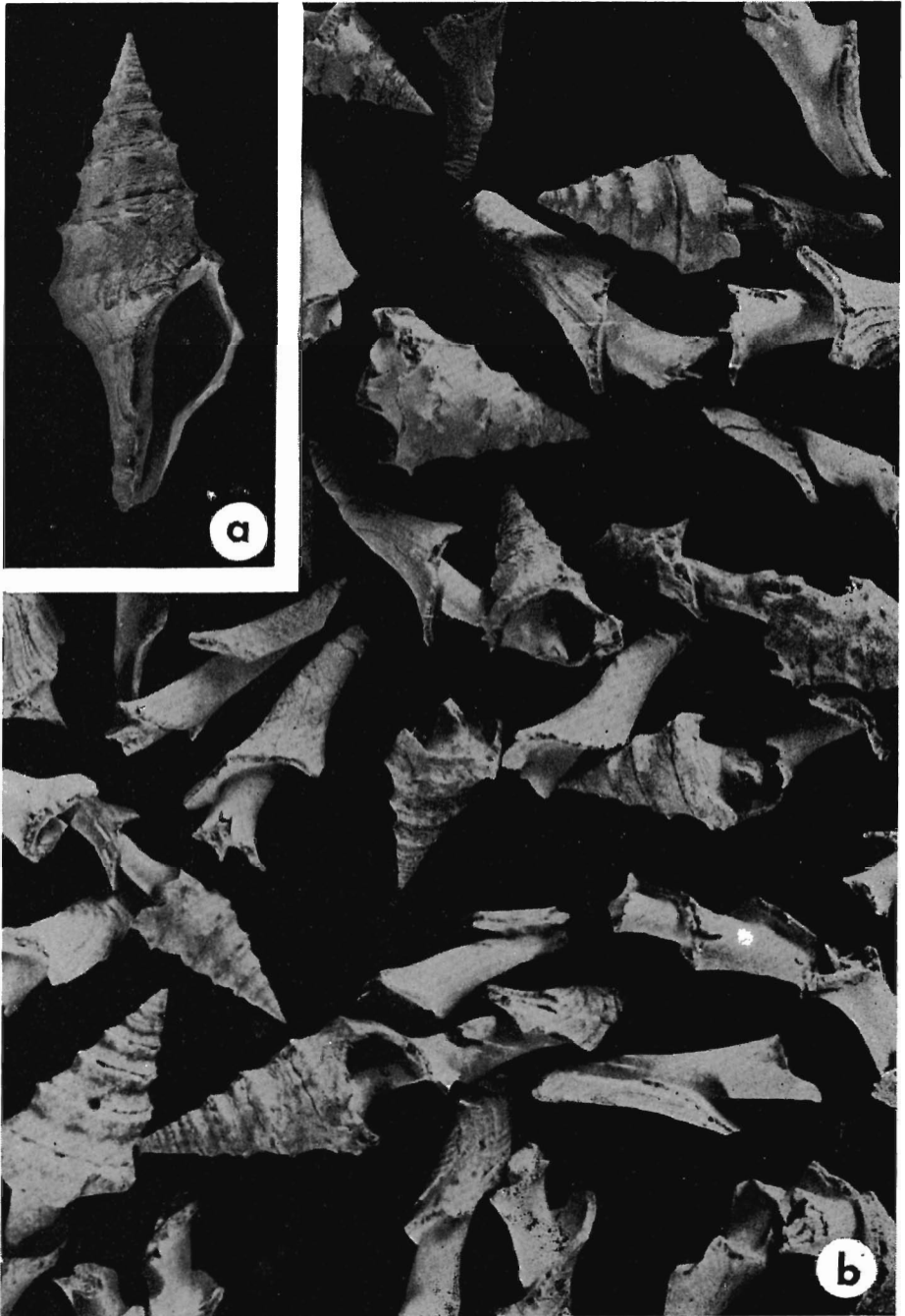
4 — Aberrant gastropod *Tenagodus (Tenagodus) anguinus miocaenicus* Cossmann & Peyrot living in a sponge (cf. Bałuk 1975, Pl. 14, Fig. 16); collected in the uppermost part of the oyster shellbed; × 8

5 — Aberrant gastropod *Parastrophia radwanskii* Bałuk (cf. Bałuk 1975, Pl. 14, Fig. 1); × 16

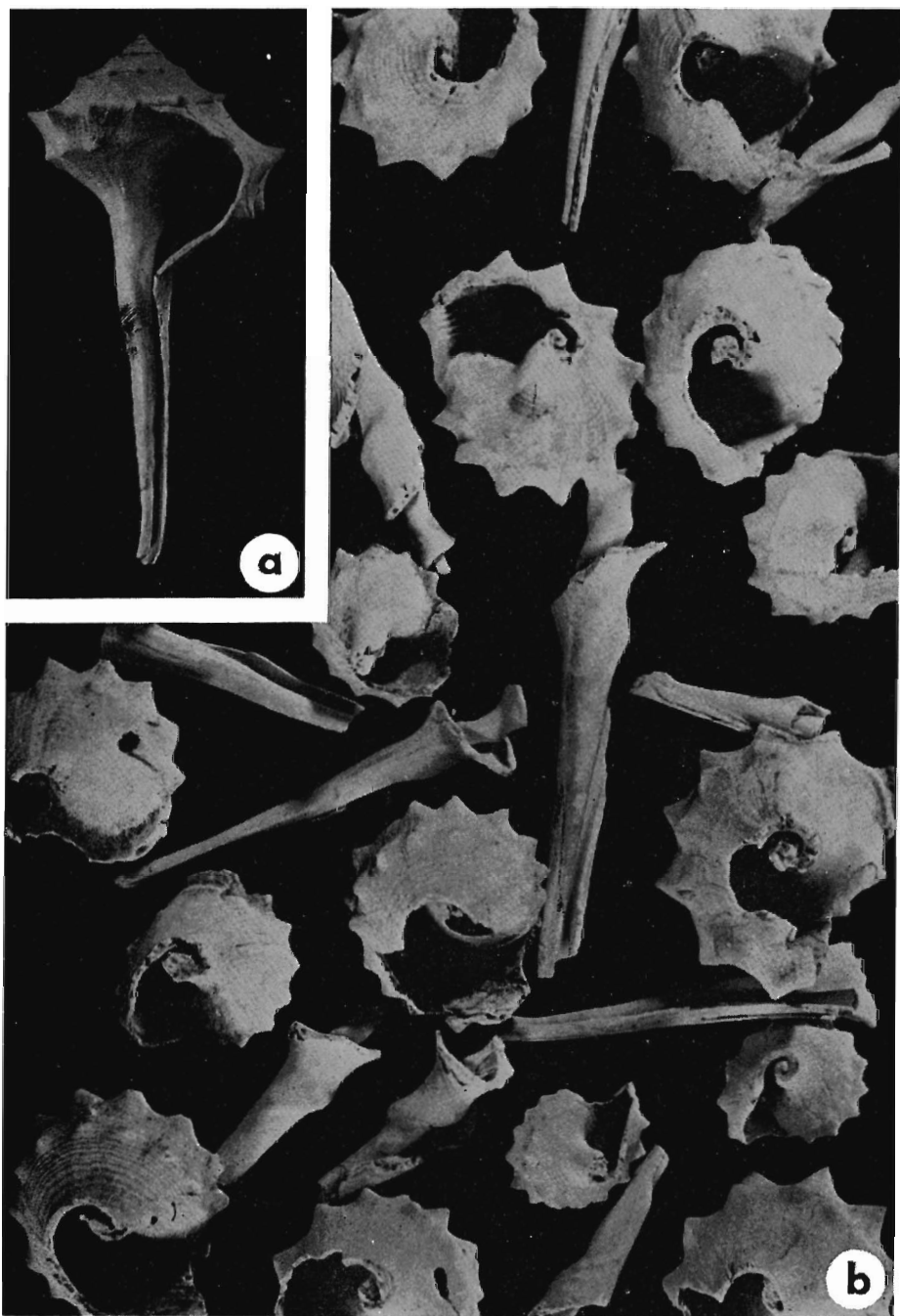
6—7 — Chitons *Cryptoplax weinlandi* Sulc: 6 head valve, 7 intermediate valve (cf. Bałuk 1971, Pl. 6); × 15

8 — Aberrant cirripedes, *Creusia sanctacrucensis* Bałuk & Radwański, domiciled in corals *Tarbellastraea reussiana* (Milne-Edwards & Haime); five well preserved, and two damaged crowns are visible, all of them having well discernible color pattern displayed by concentric stripes (cf. Bałuk & Radwański 1967, Text-fig. 3 and Pls 1—6); × 5

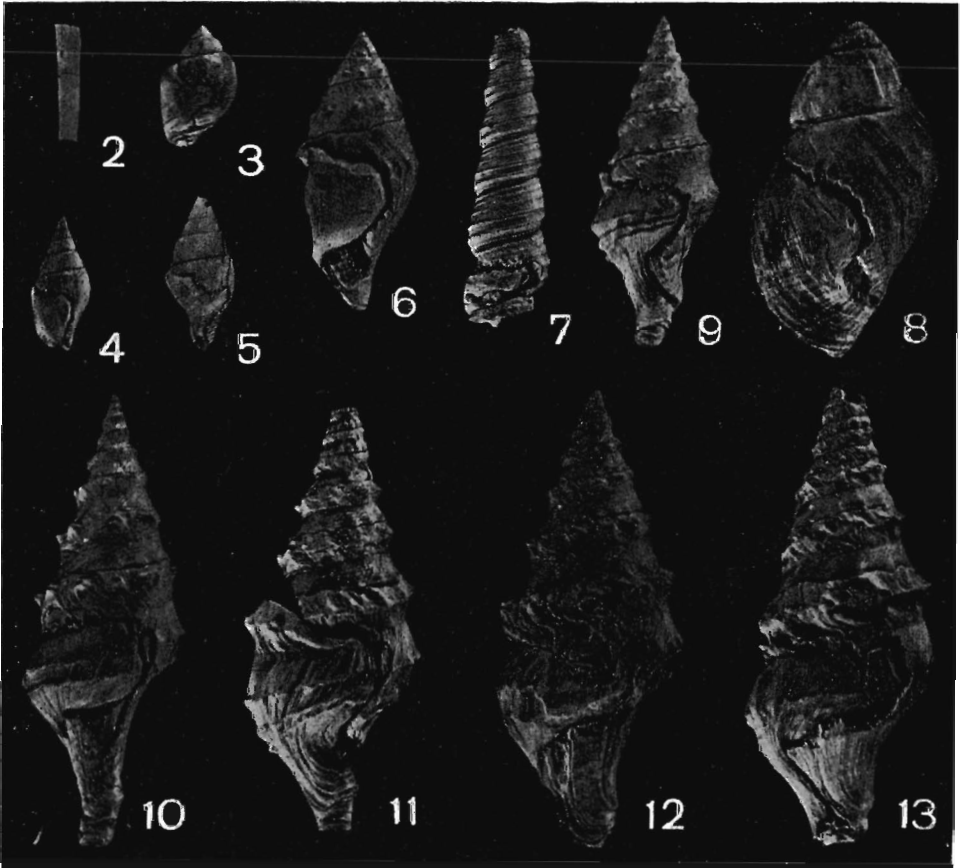
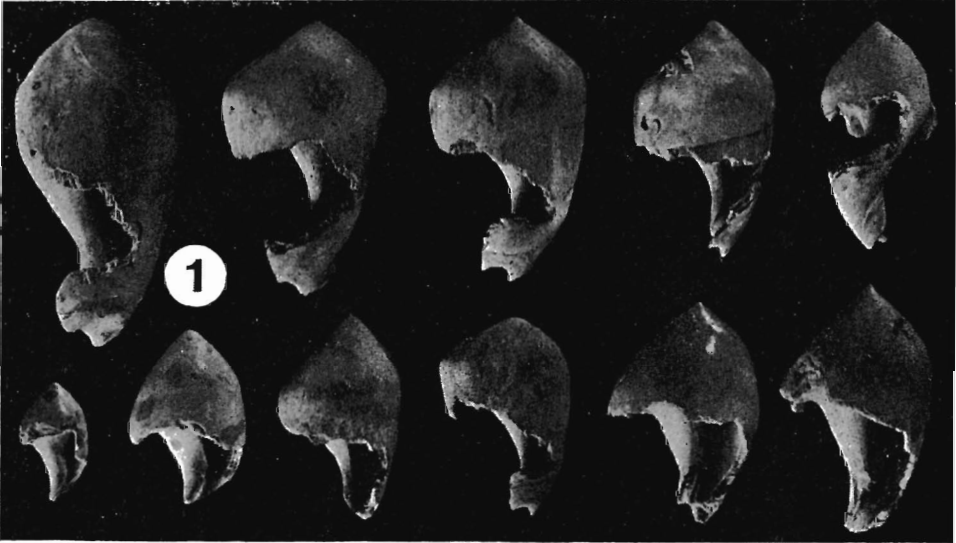




Results of activity of the hermit crabs on the shells of alive gastropods *Clavatula laevigata* (Eichwald): **a** — undamaged shell, **b** — “kitchen middens” left by the crabs on the sea floor (cf. Radwański 1977b, Pl. 11a); nat. size



Results of activity of the hermit crabs on the shells of alive gastropods *Tudicla rusticula* (Basterot): **a** — undamaged shell, **b** — “kitchen middens” left by the crabs on the sea floor (cf. Radwański 1977b, Pl. 11b); nat. size



the gastropod *Tenagodus* (*Tenagodus*) *anguinus miocaenicus* Cossmann & Peyrot, which supposedly lived within the oyster banks in the same way as in present-day environments (cf. Wenz 1939, p. 680; Bałuk 1975; Morton & Miller 1973, 2 in Text-fig. 74).

As discussed above, the vegetation of the kelp *Caulerpa* in the littoral zone is concluded from the presence (cf. Pl. 9, Figs 1—3) of the bivalved gastropods *Berthelinia krachi* Bałuk & Jakubowski. The present-day representatives of this genus live only in the habitats populated by this very kelp on which they browse (cf. Keen & Smith 1961, Bałuk & Jakubowski 1968).

The presence of some more holothurians than those indicated with sclerites by Walkiewicz (1977b), is recognized by the trophic analysis of some mollusk assemblages (Hoffman 1977) in which the gastropod genus *Eulima* was certainly adopted to ectoparasitic mode of life on sea cucumbers. Others are evident from the presence of the fish otoliths *Carapus nuntius* (Koken) recently recognized by Dr. T. Śmigiel-ska (*pers. information*), and which are attributed to the genus *Fierasfer*, the present-day representatives of which live (cf. Zei 1963) in the anus of the holothurians *Stichopus*, or rarely of *Holothuria*.

The presence of the hermit crabs, inferred from the damages in mollusk shells, is discussed in the following chapter, whereas a consideration on possible predators of the free-living bryozoans is omitted here (cf. Bałuk & Radwański 1977).

ACTIVITY OF HERMIT CRABS

The activity of hermit crabs on alive mollusks from the Korytnica basin is the best pronounced within the middle and upper part of the Korytnica Clays, i.e. within the communities II and III (cf. Text-fig. 5 and Radwański 1969, 1977b).

The most severe damage caused by hermit crabs within these communities is confined to gastropod species provided with long-siphoned shells, such as primarily *Clavatula laevigata* (Eichwald) and *Tudicla rusticula* (Basterot) whose shells are often deeply incised by crab claws, and cut into halves (cf. Pls 10—11). The resulting "wracks" of the

PLATE 12

- 1 — Results of activity of the hermit crabs on the shells of alive gastropods *Ancilla glandiformis* (Lamarck)
 2—13 — Incisions produced by the hermit crabs, and regenerated by the mollusks (cf. Radwański 1969, Pl. 37; 1977b, Pl. 12): 2 — scaphopod *Dentalium fossile raricostatum* (Sacco), and the gastropods: 3 — *Nassa schoenni* (R. Hoernes & Auinger), 4—5 — *Columbella curta* (Dujardin), 6 — *Euthria puschi* (Andrzejowski), 7 — *Turritella badensis* Sacco, 8 — *Sveltia inermis* (Pusch), 9—10 and 12 — *Clavatula laevigata* (Eichwald), 11 and 13 — *Clavatula asperulata* (Lamarck)

shells are commonly met in this interval of clay sedimentation and, if selected from the associated unattacked shells, they look like the "kitchen middens" left by satisfied crabs on the sea floor (cf. Radwański 1977b).

Nevertheless, the particular species of the Korytnica gastropods were attacked by hermit crabs to a very variable extent. Of the long-siphoned forms, the most common two *Clavatula* species, *C. laevigata* (Eichwald) and *C. asperulata* (Lamarck), became the prey in very low percentage, whereas rather uncommon *Tudicla rusticula* (Basterot) was damaged in most of the specimens collected. A low percentage of the damages is also noted in a common species *Ancilla glandiformis* (Lamarck) whose thick shells may however be nipped completely (cf. Pl. 12, Fig. 1).

When investigating the particular species, successive stages of the crab nippings are recognizable (cf. Radwański 1969, 1977b). Generally, unsuccessful for the crabs were incisions not deeper than about a half whorl, and these were regenerated by the hosts that survived. The regenerated shells, both of gastropods and scaphopods are recognizable in most of the common species (cf. Pl. 12, Figs 2—13)³. If a deeper incision by the crab had reached the mantle, and damaged it, the subsequent regeneration was associated with various anomalies in the shell shape or sculpture (cf. Radwański 1969, 1977b).

The presented results of the hermit crab activity in the Korytnica basin do not differ from those previously reported both from present-day and Neogene environments (cf. Papp & al. 1947, Boekschoten 1967, Røbba & Ostinelli 1975, Bishop 1975), being generally indicative of shallow marine conditions (cf. also Radwański 1969).

OTHER PROBLEMS

During recent investigation of various fossils from the Korytnica Clays, an attention has been paid to some new problems which may certainly be fully recognized by further research.

When studying the ecology of the collected sepioids, Bałuk (1977) noticed that these animals might have migrated into the shallows of the Korytnica basin for breeding by springtime. A similar suggestion was presented by Dr. T. Śmigieliska (*pers. information*) for some bathyal fish whose otoliths she recognized in the Korytnica Clays.

For the two animal groups, namely some regular echinoids (Mańczyńska 1977) and free-living bryozoans (Bałuk & Radwański 1977) it was stated that the clayey bottom of the Korytnica basin was their

³ Except for the two above-mentioned species, *Tudicla rusticula* (Basterot) and *Ancilla glandiformis* (Lamarck) which have never been found regenerated. These two species therefore either could not regenerate their shells, or all the crab attacks upon them were successful.

favorable environment, otherwise to that stated for the comparable present-day forms. The latter is demonstrated especially for the free-living bryozoan species *Cupuladria canariensis* (Busk) which is extant, and whose biology in present-day environments is recognized the best (cf. Lagaaij 1963, Cook 1965, Bałuk & Radwański 1977).

MEMBERS OVERLYING THE CLAYS

The members overlying the Korytnica Clays, i.e. marly sands (3 in Text-fig. 4) and red-algal (lithothamnian) limestones (4 in Text-fig. 4), both exposed the best in a sand-pit at the village Chomentow (locality 4 in Text-fig. 2) complete the sedimentary sequence of the Korytnica basin. Their lithology, facies development and paleontological content is now discussed by Radwański (1977a), and may be summarized as follows.

The marly sands that gradually appear at the topmost part of the Korytnica Clays, and make up the transitional beds c 1.5–2 meters thick (cf. Radwański 1969, Bałuk 1975), contain diversified fossils. These are mostly large foraminifers, *Heterostegina costata* d'Orbigny and single colonies of red-alga *Lithothamnium*. Typical is an assemblage of pelecypods, containing both small cockles, *Cardium paucicostatum* Sowerby, and such large-sized species as *Panope menardi rudolphii* Eichwald, *Meretrix islandicoides* (Lamarck), *M. gigas* (Lamarck), *Cardium hians danubianum* Mayer, *Crassostrea gryphoides* (Schlotheim), all of them being commonly reported by former authors (cf. Kowalewski 1930, Friedberg 1930, Radwański 1969). Recently recognized by Jakubowski (1977) is a new species of the pinnid genus *Atrina*, formerly assigned to the genus *Pinna* itself (Radwański 1969, 1970). Associated are lingulid brachiopods (Friedberg 1930, Bałuk 1975, Barczyk & Popiel-Barczyk 1977), various echinoids (Bałuk 1975, Mączyńska 1977), mostly of the genus *Echinocyamus*, starfish *Astropecten* (cf. Kowalewski 1930, Bałuk 1975), and large gastropod *Triton nodiferum* Lamarck (the latter mentioned above). Large oysters are here usually encrusted by serpulids and acorn barnacles (Radwański 1969). The bottom was, partly at least, stabilized by seagrasses (cf. chapter on seagrass vegetation; and Radwański 1977a).

Indicative of the bathymetric conditions of that member are the burrows attributable to the ghost crab *Ocypode*, the presence of which suggests a very shallow marine environment, just below or even within the intertidal zone (Radwański 1977a, b). These burrows, which occur in the upper part of the sands (cf. Radwański 1977a, Text-fig. 1), evidence therefore an extreme shallow marine (possibly, brackish-water influenced; cf. Walkiewicz 1975), or temporarily emerged episode in the history of the Korytnica basin, that is, its almost complete filling with the sediments.

The red-algal (lithothamnian) limestones which overlie the sands, record a return of marine sedimentation and a rise of sea level to about 5–6 meters (cf. Radwański 1977a). The basin was then successively

filled with algal limestones in which embedded are large cobbles and boulders derived from the shore, *i.e.*, from the Chomentow ridge (*cf.* Text-figs 1C, 2 and 3C), distant *c.* 200—300 meters (*cf.* Text-fig. 2). The largest boulders, attaining over 1 meter in their diameter, that occur in the topmost part of the limestones (*cf.* Radwański 1977a, Text-fig. 1) indicate a hurricane transport over slippery algal meadows when they have carpeted the basin almost up to sea level (Radwański 1969, 1970, 1977a, b). The boulder-bearing horizon marks the final episode of the total filling of the Korytnica basin with sediments and completes its marine history. It is presumed (Radwański 1969; *cf.* also 1974a, 1977a) that the Korytnica basin, certainly together with the shallow bays of the Holy Cross shores (*cf.* Text-fig. 1C), were then definitely excluded from the marine sedimentation which however still lasted in the deeper, open-sea facing part of the Korytnica Bay, and in the remaining areas of the Fore-Carpathian Depression.

CLIMATIC CONDITIONS

Within the organic communities of various members of the Korytnica basin there appear many animals which are indicative of tropical and/or subtropical climatic conditions. This is the best demonstrated by the taxa recognized in the Korytnica Clays, as follows.

The genus *Creusia*, adapted to living in alive colonial corals, and to which the species *C. sanctacrucensis* Bałuk & Radwański belongs (*cf.* Pl. 9, Fig. 8), is distributed at present primarily within the reef corals (*cf.* Bałuk & Radwański 1967, Ross & Newman 1973, Text-fig. 2).

The bivalved gastropod genus *Berthelinia*, which is represented (*cf.* Pl. 9, Figs 1—3) by the species *B. krachi* Bałuk & Jakubowski, lives at present in tropical and/or subtropical littoral zones only, where it browse on the kelp *Caulerpa* growing mostly inbetween rubble of strongly agitated waters just below low water level (*cf.* Keen & Smith 1961, Bałuk & Jakubowski 1968).

Of the univalved gastropods, such genera as *Terebra*, *Rostellaria*, *Architectonica*, and large-sized species of the genera *Cypraea*, *Conus*, *Strombus*, *Triton*, *Voluta* (*Volutilithes*), and *Galeodes* are commonly regarded as typical of tropical waters. The same is also true for the genus *Parastrophia*, represented (*cf.* Pl. 9, Fig. 5) by the species *P. radwanskii* Bałuk; the genus being formerly unknown in the fossil state (*cf.* Bałuk 1975), is confined at present to the tropical zone (*cf.* Wenz 1939, Bałuk 1975).

Of the chitons, represented are the species of the genera *Craspedochiton*, and *Cryptoplax*, both living at present in the tropical zone, and the latter of which, being worm-shaped (*cf.* Pl. 9, Figs 6—7), is adapted to living within crevices in coral reefs and other littoral rocks in the tropics (*cf.* Ladd 1966, Bałuk 1971).

Of the foraminifers, instructive is the species *Amphistegina lessonii* d'Orbigny, the present-day representatives of which are confined to tropical and subtropical waters (*cf.* Walkiewicz 1975, Rosenkrands Larsen 1976). The same

is said about the free-living bryozoan species *Cupuladria canariensis* (Busk) which at present has similar climatic requirements (cf. Lagaaij 1963, Cook 1965, Cadée 1975, Bałuk & Radwański 1977).

Tropical and/or subtropical character is also displayed by some holothurian sclerites which are ascribed to the present-day holothurian genera of those climatic zones (cf. Walkiewicz 1977b).

Finally, to the same climatic zones are confined the mangrove swamps (cf. Plaziat 1970), and some mollusk communities, to which the Korytnica assemblages are compared (cf. Hoffman 1977).

In the marly sands, a similar bearing upon the climatic conditions is displayed by the burrows attributable to the ghost crab *Ocypode* which at present is distributed within the tropical and subtropical zones (cf. Radwański 1977a).

A general conclusion is consequently drawn that the climatic conditions prevailing within the Korytnica basin were identical with those typical at present of the tropical and/or subtropical zones. Within the other facies of the Fore-Carpathian Depression, especially within the detrital red-algal/bryozoan facies (*Leithakalk* type of the Vienna Basin), similar climatic requirements are indicated by the large echinoids *Clypeaster*, as well as by fish. Of the latter, both teleostean genus *Scorpaena* was reported (Jerzmańska 1958), as well as various elasmobranchs (Pawłowska 1960, Radwański 1965b, Schultz 1977), of which the sharks *Hemipristis serra* Agassiz, and rays *Aëtobatis arcuatus* Agassiz are the most tropical (Radwański 1965b). All these fish, and the tropical elasmobranchs especially, may however be regarded as not the best climatic indicators, as they could migrate from warmer zones when being adult.

The tropical and/or subtropical conditions in the Miocene seas of Europe have previously been recognized by very few authors. Such conditions were concluded either from the ecological analysis of particular genera, or from the whole organic assemblage contained in the deposits studied. To the first group belong conclusions drawn on the echinoid genus *Clypeaster* investigated by Kalabis (1949) and Mitrović-Petrović (1970), as well as on the gastropod genus *Conus* studied by Hall (1964) and Davoli (1972). The second type of analysis resulted in the conclusions presented by Robba (1970) for the type Tortonian in Piedmont in Italy, and by Bohn-Havas (1973) for the Mecsek Mountains in southern Hungary. The Fore-Carpathian Depression is of all these regions situated undoubtedly the most northwardly (cf. Text-fig. 1A), but its organic communities, these from the Korytnica basin including, do not differ in their composition from those indicated from southern Europe⁴. It may therefore be postulated that no evident climatic zonation

⁴ The only exception may be ascribed to the large gastropod species *Pereiraia gervaisi* (Yézian), which is reported from south European countries (cf. Hoernes & Auinger 1879); its distribution of such a kind may however result from facies conditions (cf. Radwański 1975, p. 399).

(cf. Radwański 1975) was recognizable in the Miocene sea of Central Europe, that is, in the countries ranging from the southern Mediterranean as far as the Fore-Carpathian Depression.

The problem, whether the discussed tropical and/or subtropical conditions were prevailing only within the Miocene sea of Europe (due to, let us say, a pattern of warm currents), or they were stabilized over the Miocene land, cannot be definitely solved yet. The recent biological and ecological investigations of the Miocene terrestrial plants of Europe indicate, in any case, that tropical elements were well prospering within the then established floral communities. This is the best demonstrated (Eske Koch & Friedrich 1971) by the zingiberacean species, *Spirematospermum wetzleri* (Heer) Chandler, the present-day relative of which, *Cenolophon oxymitrum* (Schumann) Holttum, thrives only in relic sites in the jungles of Thailand. Similar climatic conditions were certainly required by the gibbons *Pliopithecus* commonly referenced from Central Europe (cf. Zapfe 1960, Kowalski & Zapfe 1974). Both this banana-like plant, and the discussed ape are reported from Poland (cf. Eske Koch & Friedrich 1971; and Kowalski & Zapfe 1974, respectively), the same as tropical/subtropical diving beetles of the genus *Canthydrus* recently found in siliceous sinter at Przeworno, Sudetic Foreland (Galewski & Głazek 1973, 1977). The climate of the Polish land outside the Fore-Carpathian Depression (cf. Text-fig. 1A—B) should therefore be regarded as not deviated from that established then in Central Europe. The Korytnica basin with its very warm water may be said to have been well suited within the tropic-influenced landscape of Central Europe.

BIOGEOGRAPHIC APPLICATION

Many of the tropical and/or subtropical elements that occur both in the Korytnica basin and in the other Miocene localities of southern and Central Europe (Tethys and Paratethys basins: cf. Text-fig. 1A), have Indo-Pacific affinities. Upon this statement, it was concluded (Radwański 1974b, 1975) that from this very region the thermophilic elements penetrated to the Miocene sea of Europe. Such a route of their spreading is also evident from the composition of animal communities in the Miocene of Asia Minor, e.g., of the Sivas region in eastern Turkey (cf. Stschepinsky 1939), and the Mut region in southern Turkey (cf. Sezer 1970), both of which yield more tropical, Indo-Pacific elements than any of the above discussed localities in Europe. The seaway connections through Turkey and the Persian Gulf regions are consequently postulated, and these were in function until the crustal upheavals resulted in their damming at the Miocene decline (Radwański 1975; cf. also Bałuk & Radwański 1977).

The Indo-Pacific affinities within the organic assemblages of Central and Southern Europe are recognizable when comparing the present-day distribution of various genera, or of species which has been extant, and when analysing the whole communities. The first is exemplified by such chitons as *Cryptoplax* (see references in Bałuk 1971), many gastropods, and even the foraminifer *Amphistegina lessonii* which the most widely distributed is in the Indo-Pacific (see references in Rosenkrands Larsen 1976). The second is demonstrated by some of the seagrass communities (see references in Hoffman 1977; cf. also Taylor 1971), and by an oyster-bryozoan-echinoid-starfish community, reported from the locality Swiniary in the Fore-Carpathian Depression (Radwański 1970, 1973, 1974a, 1975), and well comparable to that known from the Gulf of Mannar off north-western Ceylon (Herdman 1906).

The Miocene North Sea Basin which belonged to the Atlantic province (cf. Text-fig. 1A) bears also faunal influences of waters much warmer than at present (cf. Sorgenfrei 1958, pp. 414—415; Banke Rasmussen 1966, pp. 331—339; Radwański & al. 1975, pp. 252—253). These influences are certainly indicative of water inputs from the tropical or subtropical part of the Miocene Atlantic Ocean (Gripp 1961, Radwański 1975, Bałuk & Radwański 1977). These inputs were also responsible for the spreading of some thermophilic species in the Atlantic gulfs of western Europe (cf. Text-fig. 1A), and few of such species could penetrate into the Tethys and Paratethys basins, as it is exemplified by the cupuladriid bryozoans living in the Korytnica basin (cf. Cook 1965, Bałuk & Radwański 1977). These species should consequently be regarded (cf. Bałuk & Radwański 1977) as elements typical of the Atlantic province, although they lived in the sea basins so influenced by even warmer waters of the Miocene Indo-Pacific.

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