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New data on the Korytnica Basin,  
its organic communities and ecological  
relationships between species (Middle Miocene;  
Holy Cross Mountains, Central Poland)

**ABSTRACT:** The recently undertaken researches on diverse groups of fossils from the world-famous Korytnica Clays and associated deposits of the Korytnica Basin (Middle Miocene; Badenian), southern slopes of the Holy Cross Mountains, Central Poland, extend the range of recognition of organic communities, and their synecological relationships and dependence upon environmental conditions of the Basin. Reviewed and/or commented are all the recent reports, and announced are new investigations on such animal groups as anthozoans (octocorals, regenerated scleractinians), „attached” and free-living bryozoans, some inarticulate brachiopods, creusoid cirripedes, some mollusks (chitons, slipper-limpet gastropods *Crepidula*, cuttlefish), and fish otoliths. Environmental conditions are discussed in regard with the occurrence of some aberrant pelecypods (*Gastrochaena*, *Stirpulina*). Synecological relationships are demonstrated by the epibionts (hydroids *Hydractinia*, spionid polychaetes, ctenostome boring bryozoans) commensal to the hermit crabs. Indicated are also the taxa significant for tropical and/or subtropical climatic conditions, and for Indo-Pacific bioprovince affinities.

INTRODUCTION

The aim of the present paper is to review the results of recent investigations on diversified fossils, their assemblages, and/or ecological relationships from the Middle Miocene (Badenian) sequence developed within the Korytnica Basin on the southern slopes of the Holy Cross Mountains, Central Poland. This paper opens a special issue of ACTA GEOLOGICA POLONICA (Vol. 34, No. 3—4; Warsaw 1984) devoted to

the development of the Korytnica sequence, and which continues the series, the first issue of which appeared in the same journal in 1977 (ACTA GEOLOGICA POLONICA, Vol. 27, No. 2) and the second one in 1979 (ACTA GEOLOGICA POLONICA, Vol. 29, No. 3). This review comprises also general data on the geotectonic setting of the Basin and its paleogeography.

The world-famous organic world of the Korytnica Basin is still under investigation, the progressing results of which either embrace new groups of fossils or supplement the former data. In addition to the previous reports or monographs, contained in the above-indicated issues, the new accounts concern the pennatulacean corals (BAŁUK & PISERA 1984, the regenerated scleractinians (BAŁUK & RADWAŃSKI 1984a), and the "attached" bryozoans (VÁVRA 1984). The other groups of the invertebrate fossils collected from the Korytnica Clays (see BAŁUK & RADWAŃSKI 1977a, pp. 86 and 96—99; 1979a, pp. 226 and 230—231) remain under further investigation (small foraminifers, diverse corals, tubular polychaetes, ostracodes, cirripedes, gastropods, pelecypods, crinoids, ophiuroids and starfishes).

Contrary to the groups subjected to their monographing in the forthcoming future, some of the previously described soon needed a supplementary account and/or a partial revision. This happened both in the past, *viz.* for the elasmobranch and teleost fish remains (cf. SCHULTZ 1977, and 1979), and it does also at present, *viz.* for the free-living cheilostome bryozoans (cf. BAŁUK & RADWAŃSKI 1977b, and 1984b), brachiopods (cf. BARCZYK & POPIEL-BARCZYK 1977, and RADWAŃSKA & RADWAŃSKI 1984), creusoid cirripedes (cf. BAŁUK & RADWAŃSKI 1967, and 1984c), chitons and cuttlefish (cf. BAŁUK 1971, 1977, and 1984), and finally for the fish otoliths (cf. ŚMIGIELSKA 1979, and RADWAŃSKA 1984).

#### GEOLOGICAL SETTING OF THE BASIN, AND DEVELOPMENT OF ITS SEDIMENTARY SEQUENCE

The regional setting, paleogeography and development of the Korytnica Basin were presented formerly (BAŁUK & RADWAŃSKI 1977a, 1979a). The Korytnica Basin was thus characterized as a small c 5 sq km terminal part of a larger bay, the Korytnica Bay, which developed during the Middle Miocene (Badenian) transgression on the southern slopes of the Holy Cross Mountains in Central Poland.

The Middle Miocene (Badenian) transgression encroached the area to which the Korytnica Basin was confined from the Fore-Carpathian Depression in Southern Poland having all the times good seaway connections with the Vienna Basin and the Mediterranean. The transgression when reached the Holy Cross Mountains sculptured their southern slopes into a system of shallow bays which developed

within the frames of pre-Miocene valleys. The Korytnica Bay was the largest and deepest of all these bays, and the Korytnica Basin embraced a protected, terminal part of this Bay.

Within the Korytnica Basin with its depths ranging maximum between 60 and 40 meters, primarily the deposition of the Korytnica Clays took place, and the Basin, being successively filled with the Clays, has become shallower and shallower almost up to sea level (cf. BAŁUK & RADWAŃSKI 1977a, 1979c). The members overlying the Korytnica Clays, *i.e.* the marly sands and the red-algal (lithothamnian) limestones complete the sedimentary sequence which lies horizontally not being disturbed by tectonic movements except of a regional uplift of Late Badenian and/or Late Miocene age.

All members of the Korytnica sequence are extremely fossiliferous what has involved its world-wide fame since its discovery by JAŚKIEWICZ in 1787. The almost bicentennial history of Korytnica (*see* BAŁUK & RADWAŃSKI 1977a, 1979a) has been recorded by scientific effort of many generations of paleontologists who have focused their attention on the permanently increasing range of the recognized paleobiota.

On the other hand, the recognition of the paleogeography, the facies pattern and the ecological successions within the Korytnica Basin (RADWAŃSKI 1969, BAŁUK & RADWAŃSKI 1977) allowed to reference these features as the model case in some textbooks, *e.g.* on sedimentary environments (SELLWOOD 1978, pp. 298—299, Figs 10.37A and 10.37B), and on paleoecological concepts and applications (DODD & STANTON 1981, Figs 9.25 and 9.27). The general paleoecological concepts are also exemplified with the Korytnica cases by HOFFMAN (1979b, c).

The structure of the Korytnica Basin has recently been investigated with use of geophysical methods (vertical electric soundings) by SZYMANKO & WÓJCIK (1982) who postulated a geotectonic control of general frames of the Basin and, partly at least, of its Middle Miocene (Badenian) sedimentation. Geophysical data were combined by SZYMANKO & WÓJCIK (1982) with an analysis of radar images and aerial photographs of the Basin, what allowed to recognize a regional pattern of the Laramide disjunctive tectonics in the substrate and its rejuvenation during and after the Middle Miocene (Badenian) sedimentation.

The environmental studies of the members overlying the Korytnica Clays have resulted in recognition of a new site of the littoral structures (GUTOWSKI & MACHALSKI 1984), situated outside the formerly known shoreline (cf. RADWAŃSKI 1969, BAŁUK & RADWAŃSKI 1977a), and in reconstruction of sedimentary conditions and synecology of macrobenthic assemblages throughout the whole Basin (GUTOWSKI 1984). The latter work (GUTOWSKI 1984) supplements the previous synecological studies of macrobenthic assemblages from the Korytnica Clays, presented by HOFFMAN (1977, 1979a).

An importance of the seagrass vegetation during deposition of the Korytnica Clays and their littoral facies of oyster shellbeds (cf. BAŁUK & RADWAŃSKI 1977a) has recently been discussed by HOFFMAN (1979c). It has also been evidenced by studies of the "attached" bryozoans (VÁVRA 1984) and otolith-bearing teleost fishes (RADWAŃSKA 1984).

#### SYSTEMATIC STUDIES OF SOME OF THE KORYTINICA FOSSILS

To supplement the previous data on systematic studies and/or discussion of the Korytnica fossils (cf. BAŁUK & RADWAŃSKI 1979a, pp. 230—231), the reports on some chitons and gastropods are to be presented, as follows.

##### Chitons

Following the monograph of the Korytnica chitons (BAŁUK 1971), the taxonomy of which was revised by LAGHI (1977) and commented by the authors (BAŁUK & RADWAŃSKI 1979a), a special supplement and taxonomical discussion is given in a separate paper by BAŁUK (1984).

##### Gastropods

DAVOLI (1982), continuing his studies of the Miocene gastropods from Montegibbio in the northern Apennines, Italy (cf. DAVOLI 1972, 1976, 1977; see also BAŁUK & RADWAŃSKI 1979a, p. 231), has recently monographed the family Cancellariidae GRAY, 1853, and thus reviewed and taxonomically commented a few species from the Korytnica Clays (cf. FRIEDBERG 1911, 1938), viz. *Cancellaria (Bivetiella) dertonensis* BELLARDI (?= "*Bivetia subcancellata* d'ORB." of FRIEDBERG 1911), *Narona (Sveltia) dertovaricosa* (SACCO), and *Narona (Sveltia) lyrata* (BROCCHI).

Moreover, DAVOLI (1982) presented a paleoclimatic account of the family Cancellariidae GRAY, stating its tropical and/or subtropical significance, and supplementing the previous climatic data (DAVOLI 1972, 1976, 1977) on the families Conidae SWAINSON, 1840, and Terebridae H. & A. ADAMS, 1853.

The pteropod gastropods of the species *Vaginella austriaca* KITTL, 1886, have recently been illustrated from the Korytnica Clays by KRACH (1981, Pl. 1, Figs 15—18, 20; Pl. 2, Figs 21—24), although the species has earlier been reported and described from here by FRIEDBERG (1938, p. 162).

Some data on the autecology and sexual dimorphism of the slipper-limpet species, *Crepidula crepidula* (LINNAEUS), are given in a separate paper (BAŁUK & RADWAŃSKI 1985).

#### CLIMATE AND BIOPROVINCE AFFINITIES

The tropical and/or subtropical climatic conditions prevailing during sedimentation of the whole Middle Miocene (Badenian) sequence of the

Korytnica Basin (cf. BAŁUK & RADWAŃSKI 1977a, 1979a) have recently been supported by studies of some above discussed gastropods (DAVOLI 1982), inarticulate brachiopods (RADWAŃSKA & RADWAŃSKI 1984), and otolith-bearing teleost fishes (RADWAŃSKA 1984).

The Indo-Pacific bioprovince affinities of organic communities recognized within the Korytnica Basin (cf. BAŁUK & RADWAŃSKI 1977a, 1979a) have recently been discussed by HOFFMAN (1979c) for the *Turboella-Loripes* community confined to seagrass beds of the *Thalassia* type (cf. also HOFFMAN 1977, 1979a), and they have also been demonstrated for some inarticulate brachiopods (RADWAŃSKA & RADWAŃSKI 1984) and otolith-bearing teleost fishes (RADWAŃSKA 1984).

#### ECOLOGY AND TAPHONOMY OF SOME NEWLY INVESTIGATED ORGANIC GROUPS

Some of the newly investigated biota of the Korytnica sequence have a special bearing upon recognition of either environmental conditions or post-depositional events in the Basin. The first cases concern the biota, the life habit of which, controlled by the environmental conditions, have resulted in specific autecological adaptations of their skeletal morphologies to the accessible substrate. In the hereafter discussed examples of the pelecypods (*Gastrochaena* and *Stirpulina*) such an adaptation concerns the ability to construct the dwelling tubes. Post-depositional events are demonstrated by the bioerosion action of the seagrass roots upon the buried shell material. The other cases of bioerosion in dead gastropod shells are interpreted as produced by the endozoans which were commensals to the hermit crabs inhabiting those shells. The dragging of shells by the hermits caused, on the other hand, that these shells have acquired new taphonomical features.

The selected examples of the biota, the life activity of which in the Korytnica Basin was interlocking ecological and taphonomical problems will be headed in the following chapters: (i) Tube-dwelling pelecypods, (ii) Seagrass vegetation, (iii) Symbionts to the hermit crabs.

#### TUBE-DWELLING PELECYPODS

The tube-dwelling pelecypods in the Korytnica Basin were represented by the two genera: *Gastrochaena* SPENGLER, 1783, and *Stirpulina* STOLICZKA, 1870. The first, represented by the species *Gastrochaena dubia* (PENNANT, 1777) is the commonest component of the lithophocoenoses of rocky shoreline of the Basin (RADWAŃSKI 1969), the second one has not hitherto been reported from the region.

## GASTROCHAENA

The species *Gastrochaena dubia* (PENNANT) was commonly inhabiting the rocky shoreline where it left gregarious borings (RADWAŃSKI 1969). Within the shell material of the Korytnica Clays it is not so common, although in some borings the complete shells of this species are preserved (RADWAŃSKI 1969; BAŁUK & RADWAŃSKI 1977a, pp. 106—107 and Pl. 5, Figs 1—9). Agglutinaceous dwelling tubes (see RADWAŃSKI 1969, Figs 5e and 11a; WARME 1975, Fig. 11.25; CARTER 1978, Fig. 47; SAVAZZI 1982a, Fig. 8), extremely rare along the shoreline, become more frequent in shell material in which they were produced in various ways (see Pl. 1).

Usually the borings are sparsely distributed throughout the available mollusk shell, the most of which was however too thin to contain the whole boring. The pelecypod was then producing a partial boring, and completed it with an agglutinaceous tube; the latter has usually been damaged due to subsequent abrasion, and preserved is only the siphonal part of the tube (Pl. 1, Fig. 1). Such "half-borings" distributed throughout the shell indicate the shells which have long been resting on the bottom, being placed generally with their apertures downwards.

The gastropod shells resting with their heavier (adapertural) part downside, and thus with their apertures stretching upwards, were infected by the pelecypod in their interiors. This was preferentially taken by the pelecypod which has chosen it as a more protected habitat for its settling. A complete agglutinaceous tube was then produced which is more or less completely adhered to the gastropod shell (Pl. 1, Fig. 2).

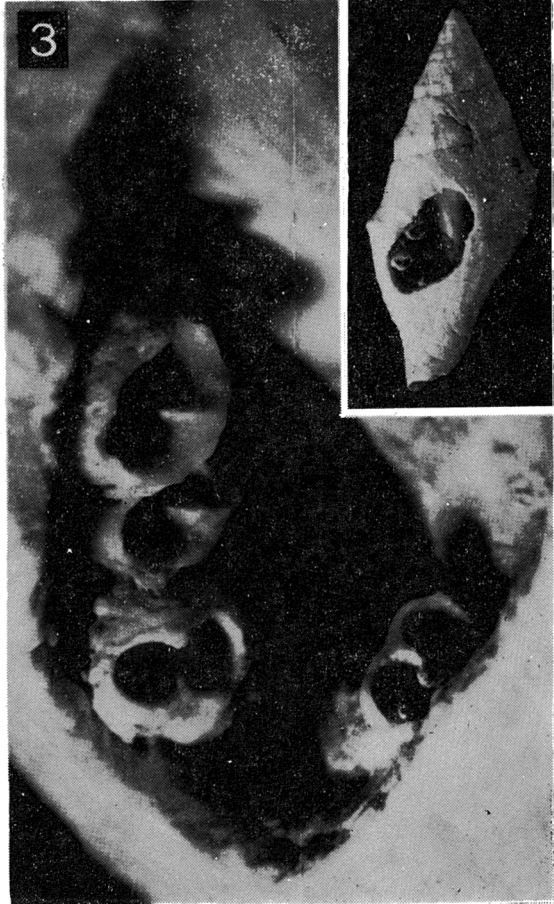
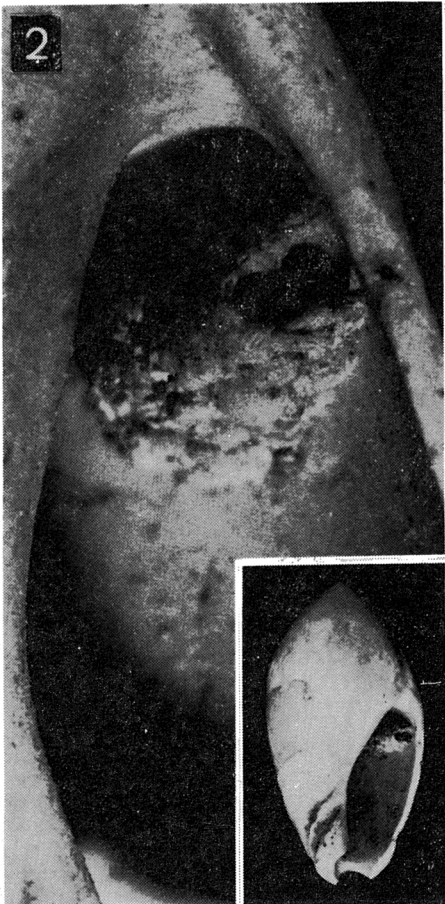
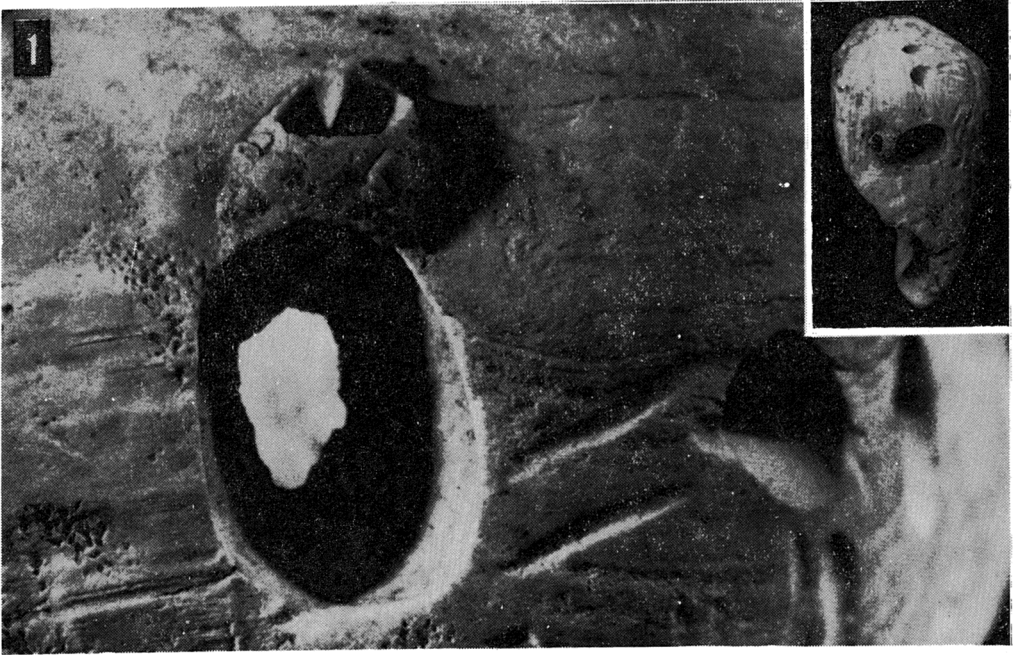
A specially favorable habitat was displayed by these gastropod shells which were partly damaged by a predatory attack (presumably by the crabs, upon the shell still occupied by the alive gastropod) to such an extent that a larger hole was produced. Through that hole the pelecypods have invaded into a protected spot, and used it for dwelling. The agglutinaceous tubes were then produced by the pelecypods living in groups, and the tubes remained also more or less completely adhered to the shell wall (Pl. 1, Fig. 3).

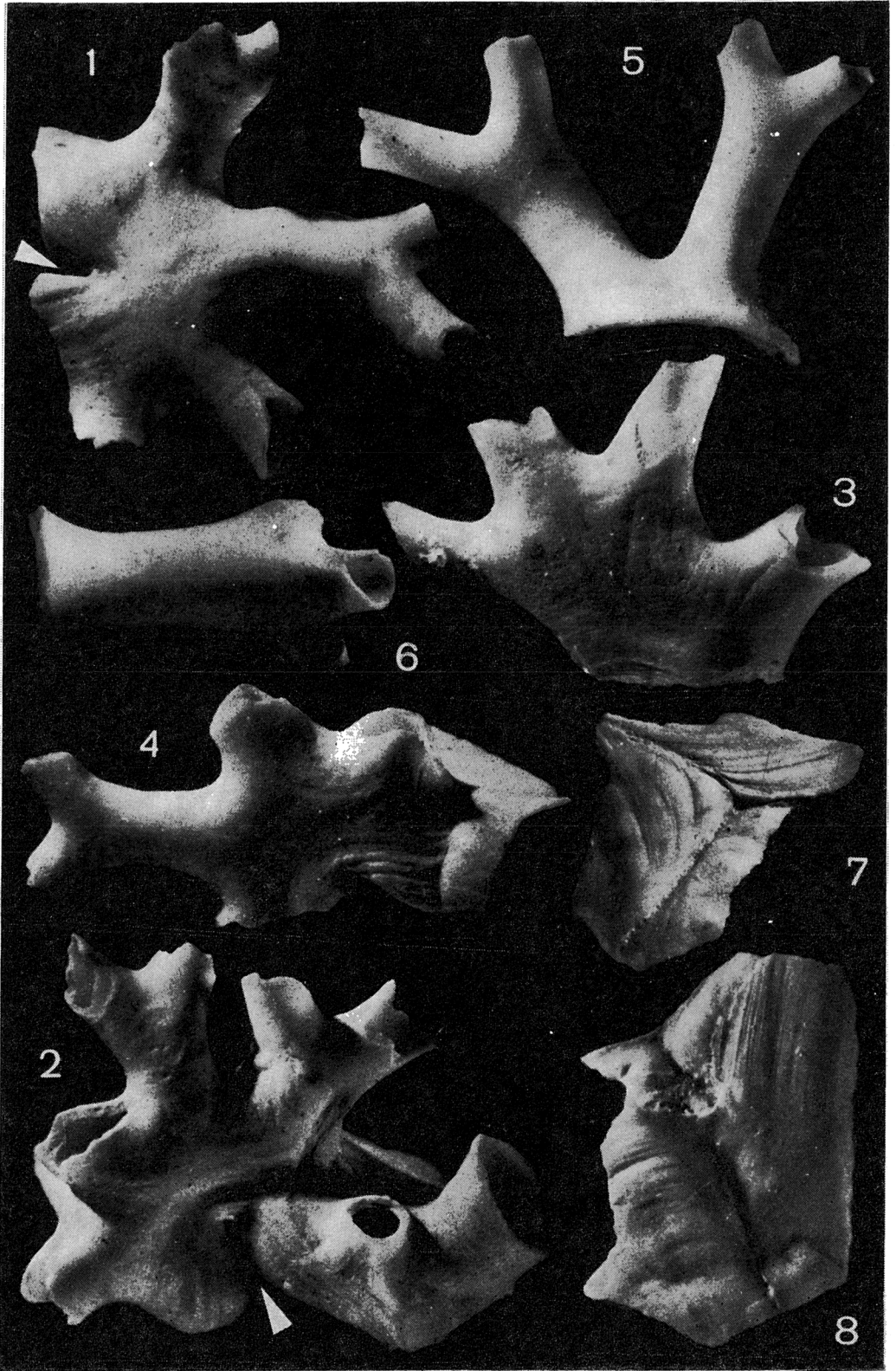
The above given examples of life activity of *Gastrochaena dubia* (PENNANT) allow to recognize the depositional history of many gas-

## PLATE 1

- 1 — Half-boring of *Gastrochaena dubia* (PENNANT) in the shell of *Ancilla glandiformis* (LAMARCK) from the Korytnica Clays (insert shows the shell magnified  $\times 1.5$ ; cf. BAŁUK & RADWAŃSKI 1977a, Pl. 5, Fig. 2): agglutinaceous tube is preserved only in its siphonal part,  $\times 10$
- 2 — Complete agglutinaceous tube of *Gastrochaena dubia* (PENNANT) in another shell of *Ancilla glandiformis* (LAMARCK) from the Korytnica Clays (insert shows the shell magnified  $\times 1.5$ ; cf. BAŁUK & RADWAŃSKI 1977a, Pl. 5, Fig. 1),  $\times 10$
- 3 — Group of complete agglutinaceous tubes of *Gastrochaena dubia* (PENNANT) around the margin of a hole in the shell of *Euthria puschi* (ANDRZEJOWSKI) from the Korytnica Clays (insert shows the shell magnified  $\times 1.5$ ),  $\times 10$

All photos taken by S. KOLANOWSKI







tropod shells contained in the Korytnica Clays. All the collected tubes are well comparable to those known in this species from diverse Neogene deposits of Europe (see FONTANNES 1881, SACCO 1901, CERULLI-IRELLI 1909, KÜHNELT 1933, SAVAZZI 1982b).

#### STIRPULINA

The presence of the genus *Stirpulina* is recognizable only upon the fragmented parts of the tubes (see Pl. 2) which occur frequently in the topmost part of the Korytnica Clays. The environmental conditions upon which this part of the Clays has been deposited, are recognized (BAŁUK & RADWAŃSKI 1977a, 1979c) as extreme shallow marine, with the bottom almost flat, covered by a pattern of dense seagrass vegetation; the sedimentary area was then some few hundred meters distant to the shoreline, either of small islands or of the mainland, in some spots fringed by a kelp bed (see Text-fig. 1). The fragmented parts of the *Stirpulina* tubes are associated here with the faecal pellets, *Tibikoia sanctacrucensis* BAŁUK & RADWAŃSKI, 1979, which are attributed (BAŁUK & RADWAŃSKI 1979c) to polychaetes related to the present-day species *Heteromastus filiformis* (CLAPARÈDE).

The collected fragments of the *Stirpulina* tubes (Pl. 2, Figs 1—8) represent their basal, more solid parts which have developed (see Text-fig.

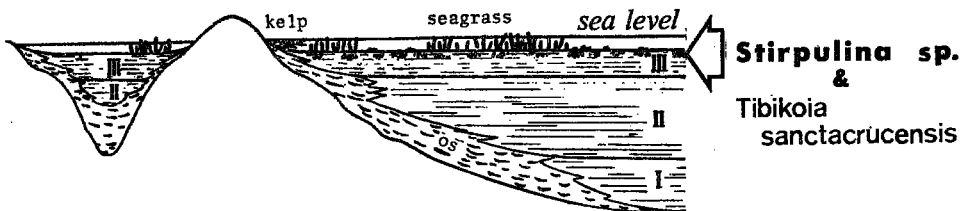


Fig. 1. Position of the layers yielding remnants of *Stirpulina* sp. within the sedimentary sequence of the Korytnica Clays (adopted from BAŁUK & RADWAŃSKI 1977, Fig. 6C, and 1979c, Fig. 1)

#### PLATE 2

Fragmented basal parts of tubes of *Stirpulina* sp. from the uppermost part of the Korytnica Clays

- 1-2 — Larger fragments of the "rootlets", showing branching tubules and the basal side of the tube with the pedal slit (arrowed)
- 3-4 — Other fragments of "rootlets" with projecting tubules
- 5 — Dichotomously branching tubules
- 6 — Triple-branching tubules
- 7-8 — Fragments of lobes covering the right valve of the pelecypod

All photos  $\times 15$ ; taken by L. ŁUSZCZEWSKA, M. Sc.

2) either as accretional lobes covering the right valve of the pelecypod (Pl. 2, Figs 7—8), or as the “rootlets” terminating the lowermost side of the tube (Pl. 2, Figs 1—6).

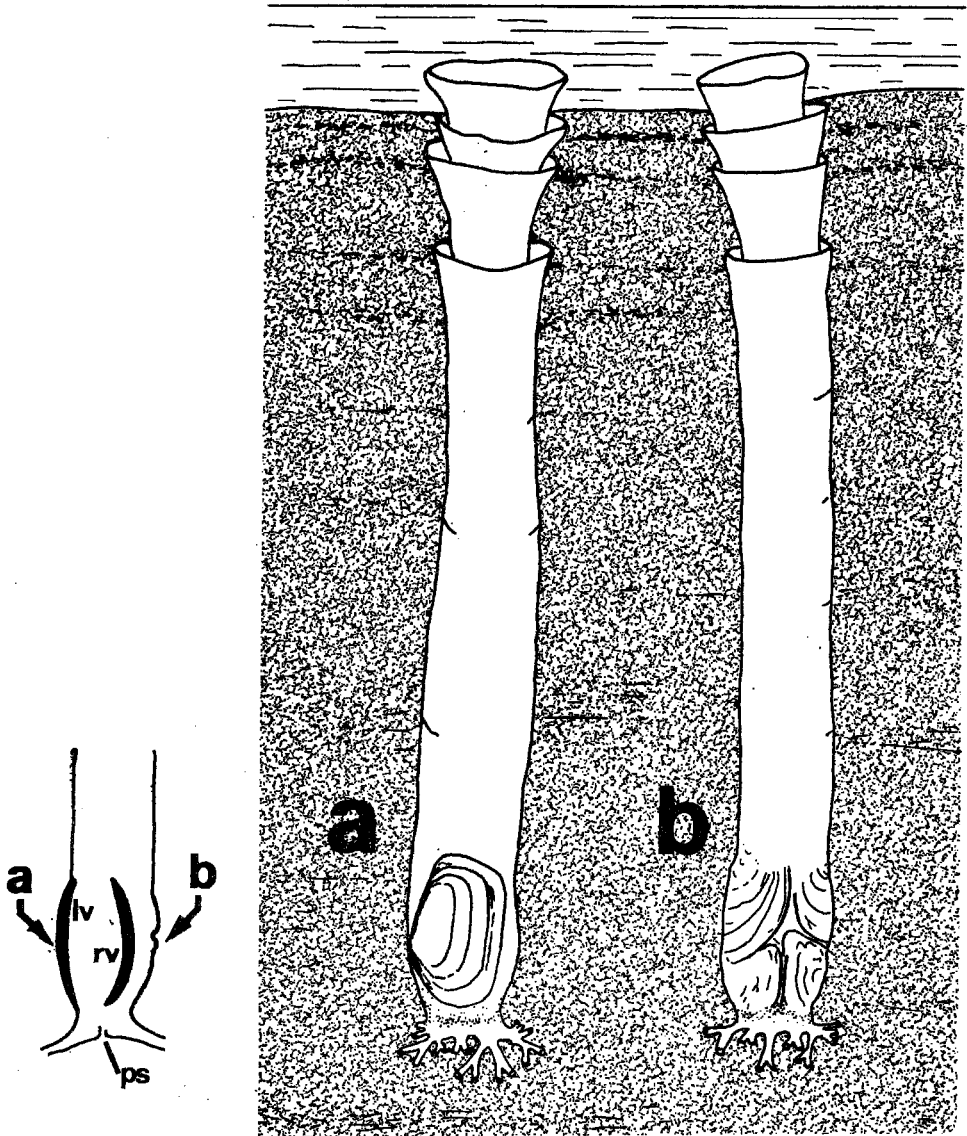


Fig. 2. Restored bottom scenery of the Korytnica environment, to show the tubes of *Stirpulina* sp. (about actual size) and their relation to the sediment/water interface: **a** — left lateral view (left valve adhered to the tube is visible), **b** — right lateral view (accretion lobes of the tube, to cover the right valve are visible)

Sketch drawing presents a longitudinal section of the tube (perpendicular to **a**), to show the left valve adhered (*lv*), the free right valve (*rv*), and the basal rootlets with the pedal slit (*ps*)

The investigated fragments of tubes, due to their characteristic features (primarily of the "rootlets"), allow to compare them well with those of the genus *Stirpulina*, although no valves are available. The collected material is thus determined only to the generic rank, as *Stirpulina* sp. Nevertheless, when comparing the preserved parts with the whole tubes known from diverse deposits of Neogene age in Europe, the species *Stirpulina bacillum* (BROCCHI, 1814) would preferably be suggested as the producer of tubes in the Korytnica Basin.

The species *Stirpulina bacillum* (BROCCHI) has hitherto been reported from the Neogene deposits of France (see FONTANNES 1881) and Italy (see SACCO 1901, CERULLI-IRELLI 1909), being also present in some localities of the Miocene deposits in the Vienna Basin (HÖRNES 1870) and Hungary (VADÁSZ 1906). The species is regarded (SACCO 1901) to include also larger forms from the Pliocene deposits of Sicily, and known under the name of "*S. bacillaris* (DESHAYES)". The investigated material matches rather to the larger forms (see SACCO 1901, p. 146 and Pl. 14, Figs 41–46), and such ones were taken into account to restore the whole tubes from the Korytnica sequence (Text-fig. 2).

The mode of construction of the tube and its function in the *Stirpulina* species has not been clarified yet. Currently, it is believed that the whole construction of the tube may move (up- and downwards) in the sediment when pumping water through the tubules of their basal "rootlets" and/or the pedal slit (see review in: CARTER 1978, pp. 71–72; SAVAZZI 1982a, b).

The selected reference data and the investigated material from the Korytnica Clays indicate that the *Stirpulina* tubes have grown in a vertical position (see Text-fig. 2), keeping pace with sedimentation, but being anchored in a constant place, and reacting to the sediment supplies by its successive prolongation upwardly. This successive prolongation is expressed by the formation of successive collars which terminate the particular growth stages. The tube is thought to have been constructed by the adult animal (contrary to the opinion of SAVAZZI 1982a, b), and an adaptation of the tube to the positive changes of sediment/water interface is realized only by further prolongation of the tube and construction of successive collars which otherwise could not be in function. The negative changes of sediment/water interface acting due to temporary winnowings of the sediment, and thus leading to a partial exposition of the tube, were followed by further outgrowths of the basal "rootlets" (cf. Pl. 2, Figs 3–6) to stabilize the tube better in the substrate. In both cases the pedal slit remains uncovered (cf. Pl. 2, Figs 1–2), whilst the lobes of the tube which cover the free right valve tend to fuse almost completely (cf. Pl. 2, Figs 7–8). An incorporation of the left valve into the tube, possible only when the pelecypod was adult, and a nearly constant diameter of particular tubules of the basal "rootlets" are additional premises to support an opinion on the tube construction by the mature specimens.

The association of *Stirpulina* sp. and the faecal pellets *Tibikoia sanctacrucensis* within the topmost part of the Korytnica Clays (Text-fig. 1) suggests an explanation of the total damage of the *Stirpulina* tubes in the environment. The present-day polychaete species *Heteromastus*

*filiiformis* (CLAPARÈDE) to whose Miocene relatives these faecal pellets are attributable, lives under intertidal and/or shallowest subtidal conditions (see references in: BAŁUK & RADWAŃSKI 1979c) where it feeds 10 to 20 cm below the sediment surface and thus it is responsible for an almost complete bioturbation of the deposit (CADÉE 1979). This reworking and/or action of hydrodynamic agents in this extremely shallow marine environment fully explains the damage of more delicate parts of the *Stirpulina* tubes, the more solid portions of which remained as a synsedimentary residuum within the sediment or on its temporary surfaces.

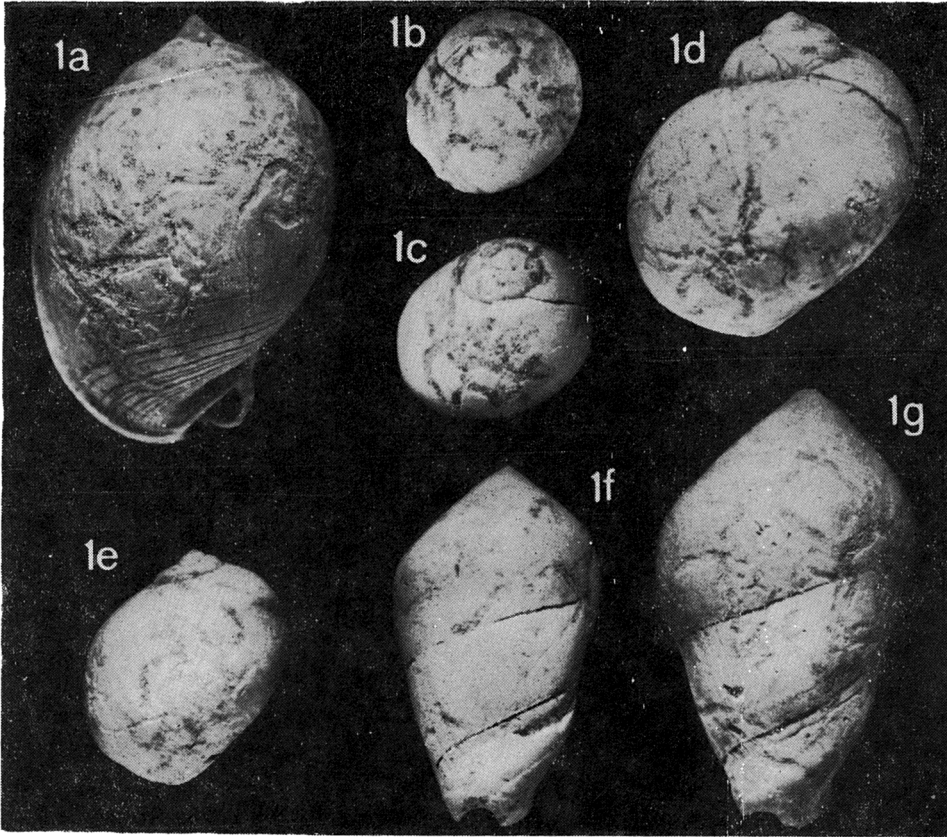
#### SEAGRASS VEGETATION

The seagrass vegetation, the general meaning of which for the depositional environment of the Korytnica Clays was reviewed above, has also resulted in the origin of post-depositional features in mollusk shells embedded in the sediment. These are the etchings (RADWAŃSKI 1977) produced by the roots of seagrasses, the structures well comparable to those of the present-day turtle grass (cf. HOFFMAN 1977, 1979a, c; RADWAŃSKI 1977; BAŁUK & RADWAŃSKI 1977a, 1979a, c).

The seagrass etchings are especially well discernible on the best preserved gastropod shells, the lustrous surface of which has not been damaged by syn-depositional abrasion and/or bioerosion (Pl. 3, Figs 1a—1g). Such shells evidence their rapid burial (contrary to that demonstrated e.g. by shells infected by *Gastrochaena dubia*) and subsequent bioerosion by roots penetrating through the sediment.

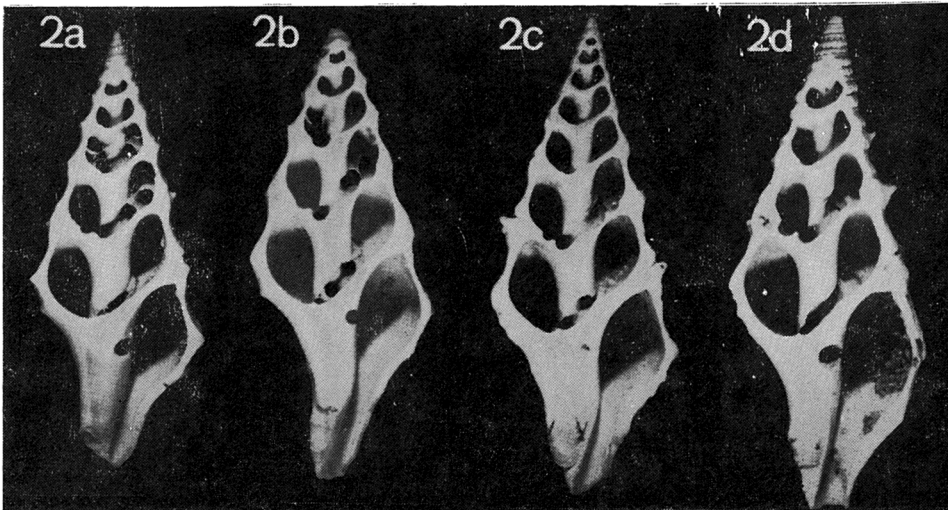
#### SYMBIONTS TO THE HERMIT CRABS

Previous investigations of some borings in dead gastropod shells from the Korytnica Clays (KERN 1979, BAŁUK & RADWAŃSKI 1979b) allowed to recognize their producers as the symbionts to the hermit crabs occupying, temporarily at least, these shells. It is evidenced by the ichnofossil *Helicotaphrichnus commensalis* KERN, GRIMMER & LISTER, 1974, distributed as half-boring and half-constructed double-running tube along the columella (Pl. 3, Figs 2a—2d), and well comparable to the present-day species of some spionid polychaetes commensal to the hermits (KERN 1979). The same is interpreted (BAŁUK & RADWAŃSKI 1979b) for the boring ctenostome bryozoans, *Spathipora* sp., *Terebripora* sp., and *Penetrantia* sp., often associated with *Helicotaphrichnus commensalis*, and distributed throughout the circum-apertural part of the gastropod shells. Some bryozoan-infected gastropod shells, especially the more solid



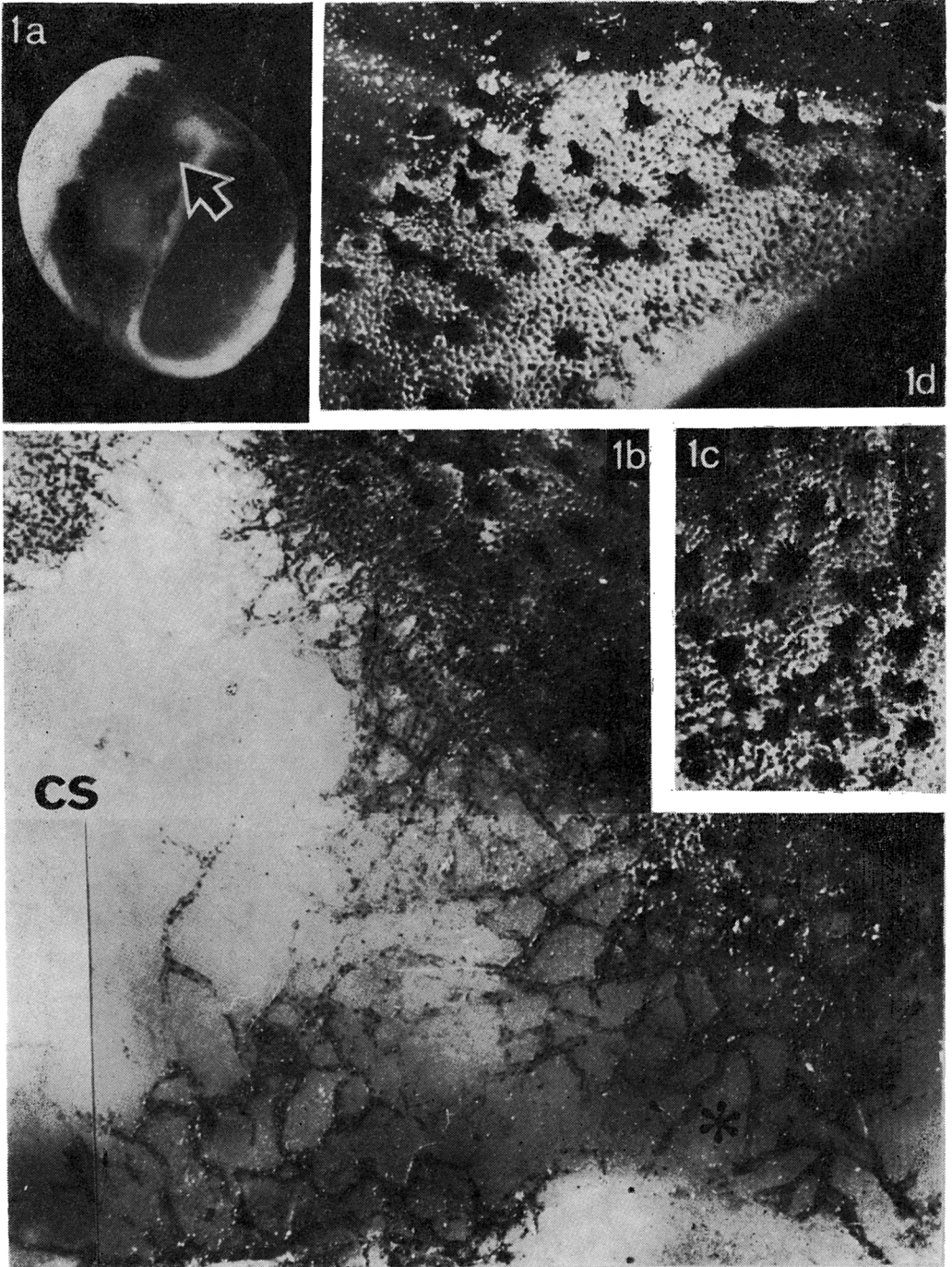
Etchings produced by seagrass roots in the shells of gastropods from the Korytnica Clays: **1a** — *Cassis miolaevigata* SACCO, **1b-1c** — *Natica josephina* (RISSO), **1d** — *Natica millepunctata* LAMARCK, **1e** — *Polynices redempta* (MICHELOTTI), **1f-1g** — *Ancilla glandiformis* (LAMARCK); all about actual size

Photos taken by B. DROZD, M. Sc.



Ichnofossil *Helicotaphrichnus commensalis* KERN, GRIMMER & LISTER in the shells of gastropods from the Korytnica Clays: **2a-2b** — *Clavatula laevigata* (EICHWALD), **2c-2d** — *Clavatula asperulata* (LAMARCK); all about actual size

Photos taken by S. KOLANOWSKI

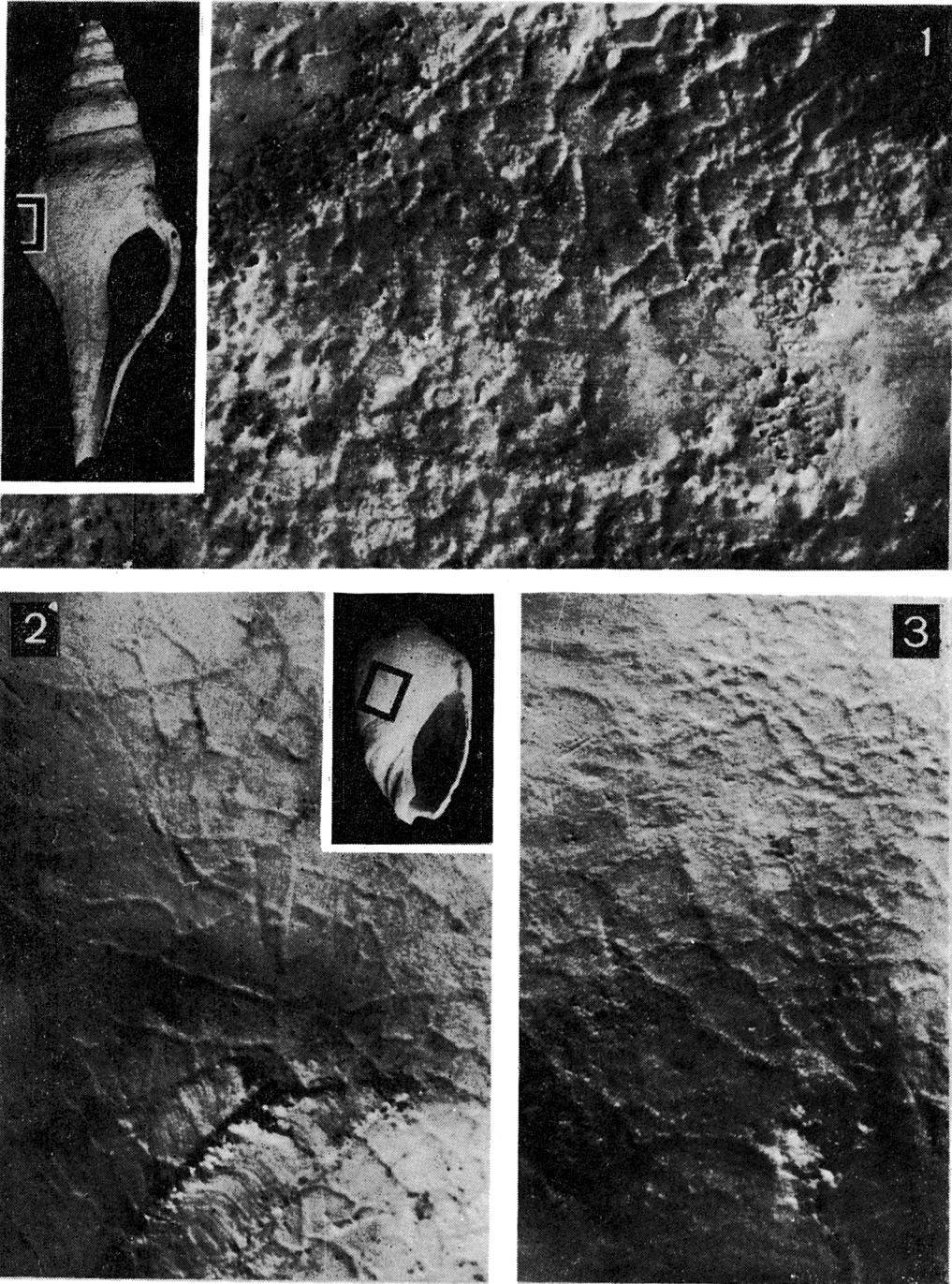


*Hydractinia echinata* (FLEMING) encrusting the circum-apertural part of a naticid shell; Hikkaduwa coast, Ceylon (coll. A. RADWAŃSKI, 1975)

1a — General view of the naticid shell (twice magnified); 1b — Organic exoskeletons of rhizomes in the marginal part of the colony, situated at the middle of the inner lip and near the callus (cs) of the shell (asterisked point is arrowed in Fig. 1a); 1c — Peridermal mat with spines in the more central part of the colony (see upper right in Fig. 1b); 1d — Another fragment of the peridermal mat with spines, not obstructed by the hermit's dragging

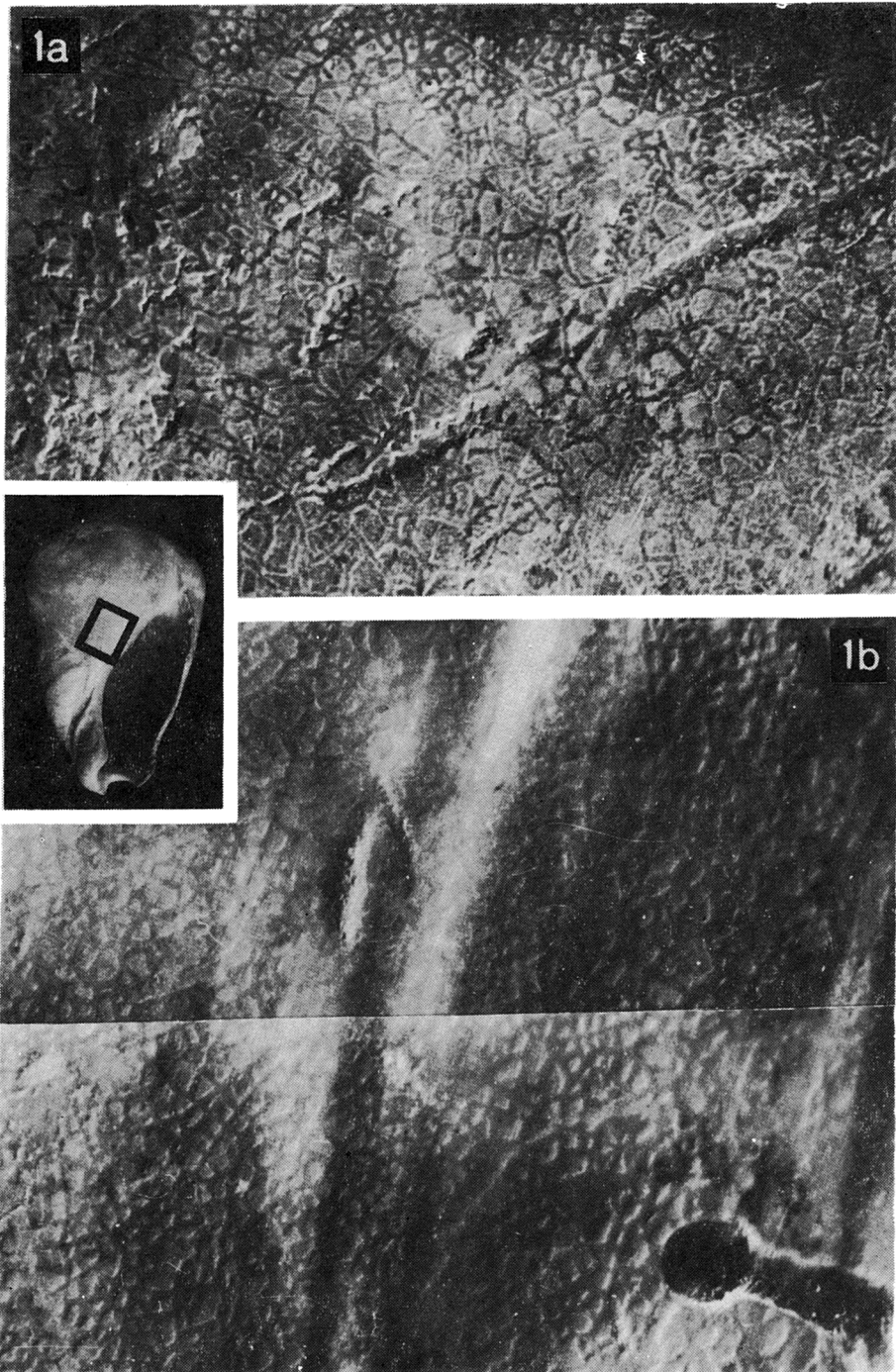
Colony fragments X15; photos taken by L. ŁUSZCZEWSKA, M. Sc.

Photo of the shell taken by K. ZIELIŃSKA



Etchings attributable to the hydroid related to the present-day species *Hydractinia echinata* (FLEMING), in the shells of gastropods from the Korytnica Clays: 1 — *Fusus hoessi* PARTSCH (insert shows the shell in actual size, and the place of photo); 2 — *Ancilla glandiformis* (LAMARCK) (insert shows the shell in actual size, and the place of photo); 3 — another specimen of *Ancilla glandiformis* (LAMARCK)

All etchings  $\times 15$ ; photos taken by L. ŁUSZCZEWSKA, M. Sc.  
 Photos of the shells taken by K. ZIELIŃSKA



**1a-1b** — Etchings attributable to the hydroid related to the present-day species *Hydractinia echinata* (FLEMING) in another shell of *Ancilla glandiformis* (LAMARCK) from the Korytnica Clays (insert shows the shell in actual size, and the place of photo in Fig. 1a; photo for Fig. 1b is taken on the opposite side of the shell, cf. Text-fig. 3)

Etchings  $\times 15$ ; photos taken by L. ŁUSZCZEWSKA, M. Sc.  
 Photo of the shell taken by K. ZIELIŃSKA



and thicker ones as, for instance, of *Ranella marginata* (MARTINI), are additionally provided with wearing marks which developed due to the dragging of the shell by a hermit, and sometimes they are also provided with an incision on the outer lip of the shell which resulted from its rubbing by the hermit's claw (see BAŁUK & RADWAŃSKI 1979b, p. 249 and Pl. 8, Fig. 2).

To the same category of the hermit-crabs' symbionts belonged the producers of very delicate maze-like arranged etchings (Pls 5—6), the pattern and shape of which are almost identical with those produced by the present-day hydroid species *Hydractinia echinata* (FLEMING), widely distributed all over the oceans (cf. MERRILL 1967), selectively confined to the shells inhabited by hermit crabs (cf. SCHIFSMA 1935, JENSEN 1970, MERCANDO & LYTLE 1980, KARLSON & CARIALOU 1982), and exemplified herein by a specimen from the coast of Ceylon (Pl. 4).

In this present-day specimen (see Pl. 4), a colony of *Hydractinia echinata* (FLEMING) encrusts the circum-apertural part (especially the inner lip) of a naticid shell (Pl. 4, Fig. 1a). The thinnest, marginal part of the colony, is preserved as a network systems of the organic exoskeletons of rhizomes (stolons), i.e. of the hydrorhizae (Pl. 4, Fig. 1b), which towards the colony center fuses into the peridermal mat with numerous spines (Pl. 4, Figs 1c—1d). The rhizomes well discernible in the outermost part of the colony, make up denser and denser, either branching or anastomosing tangle, due to which the meshes of the network become filled up.

Fig. 3

Supposed view of a Korytnica hermit crab carrying the shell of the gastropod *Ancilla glandiformis* (LAMARCK), encrusted by the commensal hydroid related to the present-day species *Hydractinia echinata* (FLEMING); the shell is the same as inserted in Pl. 6; slightly magnified over actual size



The patterns identical to those of the discussed rhizomes, and recognizable on some Korytnica shells are therefore interpreted as produced by a hydroid closely related to the indicated present-day species, *Hydractinia echinata* (FLEMING). This hydroid also lived preferentially in the circum-apertural parts of the gastropod shells (Pl. 5, Fig. 2), although some specimens were covering the accessible shell almost wholly (Pl. 5, Fig. 1 and Pl. 6), as it happens also in the present-day colonies. In particular specimens the pattern of rhizomes varies in regard to its density: in some cases it is the same as in the present-day example (compare Pls 4 and 5), in others (e.g. Pl. 6) it is evidently denser, due to a greater number of

the rhizomes. The latter case may correspond either to the age of the colony, or to the variable mode of the adherence of rhizomes to the shell substrate.

All the Korytnica specimens are the etchings in the shell substrate (cf. RADWAŃSKI 1977). Within an etching, the rhizome pattern is less etched than the meshes of the network. It is therefore thought that the rhizomes in the bioerosion processes were sharing a lesser role than the remaining part of the colony.

In the present-day example (Pl. 4), the discussed part of the colony which displays the best the pattern of rhizomes (Pl. 4, Fig. 1b), extends at the middle part of the inner lip of the naticid shell, just near its callus which remains uncovered by the *Hydractinia* colony. Both these areas are the places being easily worn when the shell was dragged by the hermit over the bottom. This certainly explains a weaker development of the *Hydractinia* colony in these areas. In other parts of the discussed shell the *Hydractinia* colony is much thicker and the rhizome pattern remains not discernible. Within the Korytnica material, distinct marks attributable to a wearing due to the hermit's activity are present in the more solid shells, especially of *Ancilla glandiformis* (LAMARCK), which are the most commonly infected by the hydroids (see Pl. 6 and Text-fig. 3).

The presented data show that the etchings attributable to the hydroids related to the present-day species *Hydractinia echinata* (FLEMING) are a significant key for the recognition of ecological relationships between species. These hydroids are interpreted to have lived in the Korytnica Basin, exclusively on the shells occupied by the hermit crabs to which they have become the symbionts.

Recently, the hermit-crab shells acting as a substrate for an organic settlement have been claimed to be a spatial refuge for solitary epizoans (STACHOWITSCH 1980, KARLSON & CARILOU 1982). In the Korytnica case this may be evidenced by the spionid polychaete species responsible (cf. KERN 1979) for producing the ichnofossil *Helicotaphrichnus commensalis*. The boring ctenostome bryozoans (cf. BAŁUK & RADWAŃSKI 1979b) and the discussed hydroids, both confined to the hermit-crab shells and unknown from other habitats (e.g., shorezone rocks) of the Korytnica Basin, evidence that such a spatial refuge was at the Middle Miocene time actual also for the colonial organisms.

#### INTERPRETATION OF SOME ECOLOGICAL DATA

When the data on bathymetric requirements of bryozoans are taken into account, it becomes evident that the bryozoan-bearing communities were spreading in the Korytnica Basin at depths much smaller than needed by the comparable present-day forms. This is indicated both by the attached and free-living colonies. The attached bryozoans from the oyster shellbed being a littoral facies of the Korytnica Clays (upper part

of community II, and community III of BAŁUK & RADWAŃSKI 1977a), are presently interpreted by VÁVRA (1984) as confined to depth "perhaps 30—50 m", the value being almost twice greater than evidenced by the other ecological groups (see BAŁUK & RADWAŃSKI 1977a, Text-fig. 5 and pp. 100—101; 1977b, p. 152). The free-living species *Cupuladria vindobonensis* BAŁUK & RADWAŃSKI, belonging to the "C. canariensis group" of former authors (cf. BAŁUK & RADWAŃSKI 1984b) and coming primarily from the topmost part of the Korytnica Clays (community III of BAŁUK & RADWAŃSKI 1977a), was confined to bottoms of extreme shallow depths, from a few meters to almost nil (see also BAŁUK & RADWAŃSKI 1977b, p. 152). The latter data are much deviated from those known in the present-day biotopes typical of the "C. canariensis group" of species (see BAŁUK & RADWAŃSKI 1977b, 1984b). This remarkable difference has recently been discussed by HOFFMAN (1979b) as an example of the ecological evolution of the cupuladriid bryozoans in regard with their bathymetric requirements and resulting life habitat. Probably, this is also a case with the attached bryozoans investigated by VÁVRA (1984) unless the data on distribution of the present-day forms are still very incomplete.

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