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MIDDLE MIOCENE RHODOLITHS FROM THE KORYTNICA BASIN  
(SOUTHERN POLAND): ENVIRONMENTAL SIGNIFICANCE  
AND PALEONTOLOGY

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Rhodoliths from the Middle Miocene (Badenian) deposits of the Korytnica Basin are analysed in terms of environment-related internal features (symmetry, massiveness, growth forms of algae, borings, algal species composition and distribution). Differences in internal structure and distribution of dominant species in the rhodolith populations from Korytnica and Chomentów reflect environmental differences between the two parts of the Korytnica basin. Dense, symmetrical rhodoliths built frequently of thin thalli, with frequent epibionts and rare borings are typical of the shallower part of the basin (Chomentów). Porous, asymmetrical rhodoliths, built mainly of thick thalli, with less frequent epibionts and common borings prevail in the deeper part of the basin (Korytnica). In the systematic part of the paper 26 species of 7 genera (*Archaeolithothamnium*, *Palaeothamnium*, *Lithothamnium*, *Mesophyllum*, *Lithophyllum*, *Leptolithophyllum* and *Titanoderma*) are described, 7 of which are for the first time reported from the Polish Miocene.

**Key words:** rhodoliths, red algae, paleoecology, systematics, Miocene, Poland.

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#### INTRODUCTION

Rhodolith-bearing deposits are very common in the Middle Miocene of southern Poland, as well as in the whole Paratethys region. Nevertheless, they have long been neglected in detailed geological and paleontological studies, although their importance in environmental reconstructions of such deposits is quite substantial (see Bosence 1983b, Bosence and Pedley 1982, Scoffin *et al.* 1985, Studencki 1988a, Braga and Martin 1988).

The Korytnica Basin with its well known fossil fauna has for long attracted the attention of paleontologists (for reviews see Bałuk and

Radwański 1977, 1979, 1984). Most fossils groups have already received their paleontologic description, and several paleoecological studies have been done as well (Bałuk and Radwański 1977, 1984, Hoffman 1977, Gutowski 1984). On the other hand, coralline algae, one of the most common elements of the community during the later developmental stage of the basin, have not received an adequate attention. The purpose of this study is therefore twofold: first, to analyze the rhodoliths—the most common form of algal presence—as a potential tool in paleoecological and environmental reconstruction; and second, to present a paleontological description of the coralline algae—apparently the last group of fossils of the Korytnica Basin still unstudied in systematic terms.

The investigated material is housed at the Institute of Paleobiology, Polish Academy of Sciences, Warszawa (abbreviated ZPAL).

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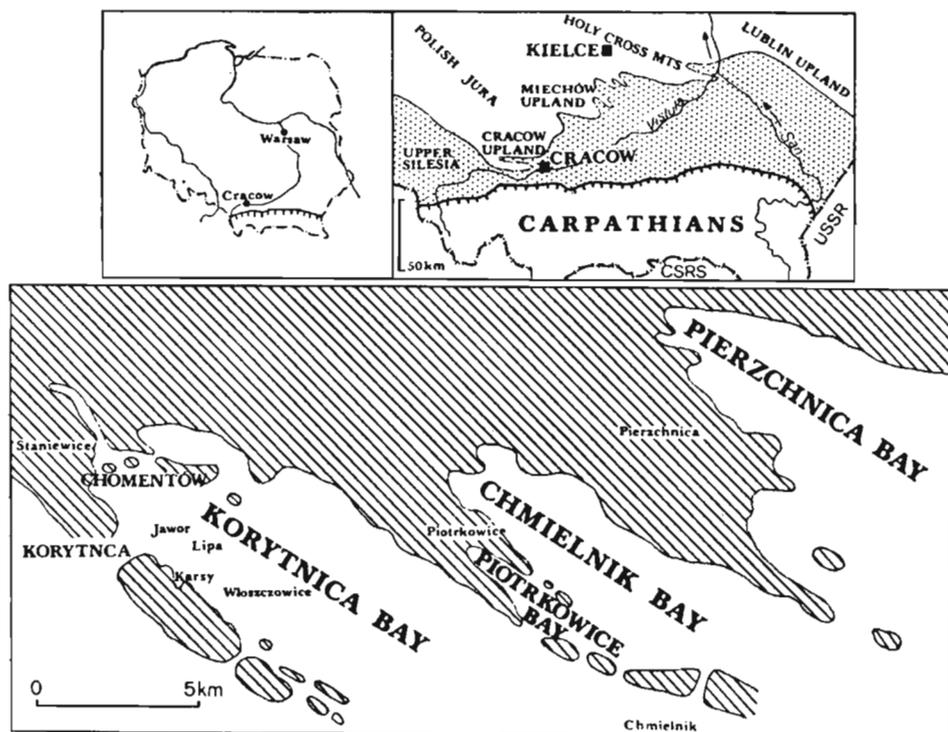


Fig. 1. Location and paleogeographic situation of the sampled rhodolith-bearing deposits (partly from Radwański 1969, modified).

## GEOLOGICAL SETTING

The Korytnica Basin is the proximal and well protected end of the larger Korytnica Bay, which developed on the southern slopes of the Świętokrzyskie (Holy Cross) Mountains (fig. 1) during the Middle Miocene (Badenian) (Radwański 1969, Bałuk and Radwański 1977). Its sedimentary infill represents nearshore deposits of the northern margin of the Carpathian Foredeep, which is in turn a part of Central Paratethys. The sedimentary sequence in the Korytnica Basin starts with brown coal-bearing deposits covered by extremely fossiliferous clays, which are the dominant sediment of the basin. They are overlain by marly sands and sandstones; coralline-algal limestones occurring around the edges of the basin terminate the sequence (figs 2—3; Radwański 1969, Bałuk and Radwański 1977, 1984, Gutowski 1984).

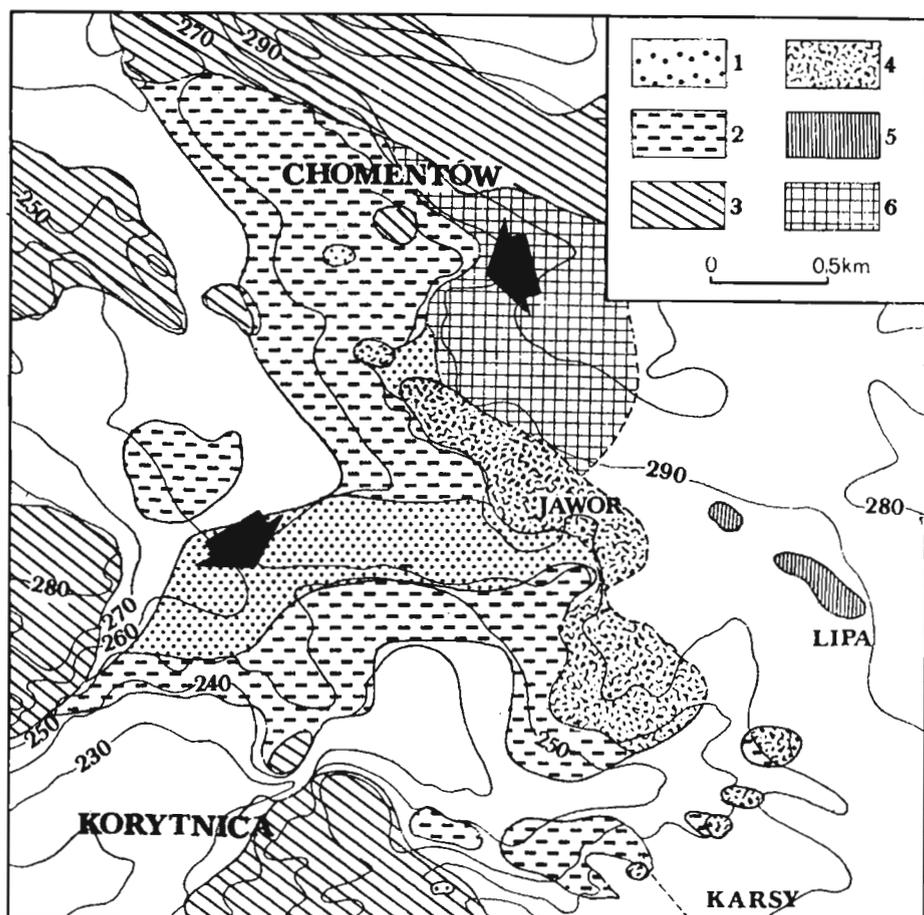


Fig. 2. Distribution of facies in the Korytnica Basin (sampling sites arrowed; from Gutowski 1984, modified). 1 sandy marls, 2 Korytnica clays, 3 Jurassic substrate, 4 gravels, 5 sandy coralline-algal deposits with bentonites, 6 coralline-algal limestone.

For the purpose of this study, rhodoliths have been collected from (i) sands and sandstones in the Korytnica Basin and from (ii) coralline-algal limestones in Chomentów (see fig. 2).

(i) The marly sands and sandstones, fine to medium grained, are about 7 meters thick in Korytnica and contain numerous large foraminifers (*Heterostegina* and *Amphistegina*), rhodoliths and other coralline-algal detritus, as well as numerous horizons with mollusk accumulations (mostly molds and imprints); the sequence has been recently interpreted as shallow water (about 10 meters depth) deposits, structured mainly by storms (Gutowski 1984).

(ii) The coralline-algal limestones from Chomentów are about 5 meters thick and show no clear stratification. They are partly isochronous with

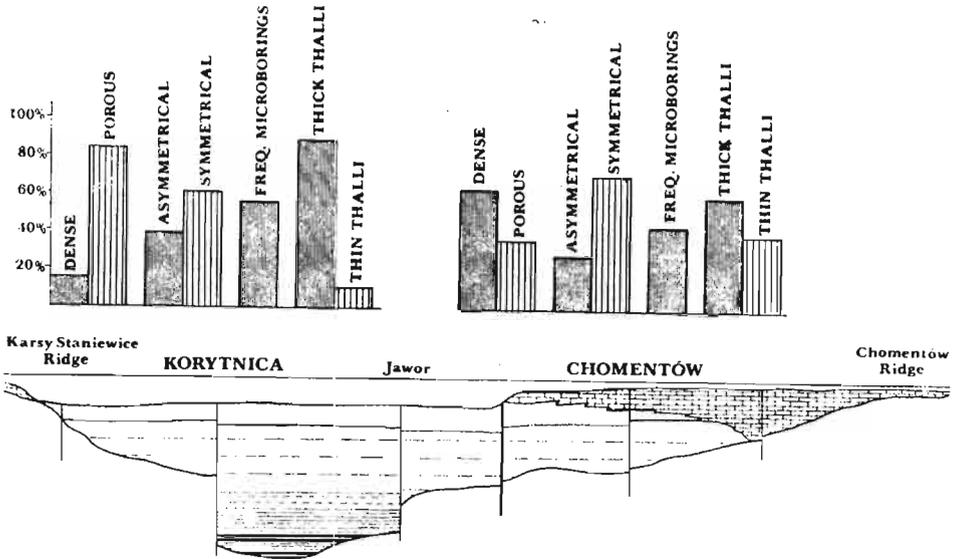


Fig. 3. Cross-section of the Korytnica Basin showing its structure and distribution of the Miocene deposits (from Gutowski 1984, modified); above, the main features of the investigated rhodolith populations are shown.

but partly overlay the sands and sandstones from Korytnica (cf. Radwański 1969, Gutowski 1984). These limestones are composed mostly of coralline-algal branched thalli (mostly broken), subordinate rhodoliths, numerous large foraminifers (*Heterostegina* and *Amphistegina*), bryozoan colonies, fragments of oysters and scallops, rare corals and other biogenic remnants embedded in a micritic, somewhat marly matrix with admixture of poorly rounded quartz grains. All these grains amount to 40–60% of the rock on the average (Szczuchura and Pisera 1986). Strongly bored pebbles of Jurassic limestones, which form the substrate of the Miocene deposits in this area, are common in places (Radwański 1969). According

to Radwański (1969) and Gutowski (1984), these deposits were formed as a nearshore bank in extremely shallow marine setting, approaching even the sea level.

## METHODS

Over 100 rhodolith specimens were cut and their internal structure was investigated on polished surfaces. The structure and composition of the algae were investigated in over 100 oriented thin sections. Most rhodoliths were also measured along three perpendicular axes and the results used for shape analysis. All the investigated rhodoliths are relatively small, not exceeding 100 mm in size in Korytnica (average about 60 mm), and 76 mm in Chomentów (average 50 mm).

## CHARACTERISTICS OF RHODOLITHS

The rhodoliths have been analyzed with respect to several criteria, viz. shape, internal structure, algal species diversity, massiveness, associated microbiota (microborers and encrusters), and algal thallus thickness. The results reveal some meaningful differences between the two studied populations of rhodoliths, thus indicating different environmental conditions of their growth.

### Shape

Both the analyzed rhodolith populations show strong dominance of two shape classes, i.e. spheroidal and ellipsoidal, with the same distribution pattern of these two forms in each population (fig. 4). Ellipsoidal rhodoliths are most easily transported, even more easily than spheroidal ones (Bosence 1983b), but shape itself is quite useless as the criterion because certain rhodoliths externally susceptible to rolling clearly show unidirectional growth, thus evidencing their stability.

### Massiveness

Two types of rhodolith could be easily distinguished, (i) porous, with great amount of primary growth-framework voids between crusts, branches and columns (pl. 1: 1—3, pl. 2: 2, pl. 3: 1); and (ii) massive, compact, with low primary porosity (pl. 1: 4—5, pl. 2: 1, pl. 3: 2, pl. 4: 1, 5). There is a clear distinction between the two analyzed localities in this regard: porous rhodoliths strongly dominate in Korytnica, while dense ones prevail in Chomentów.

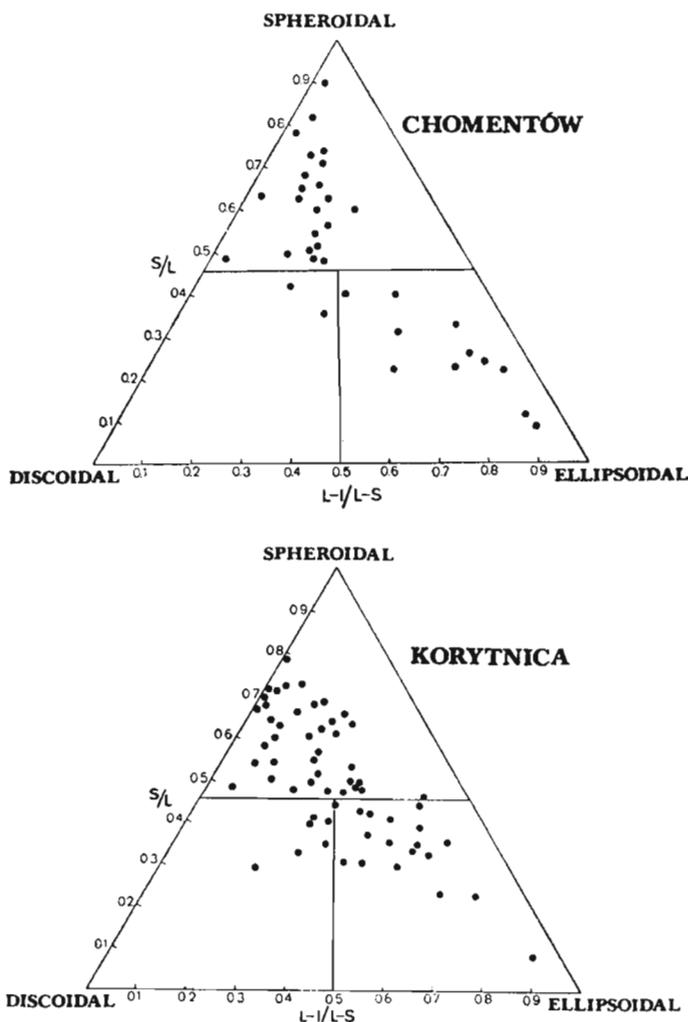


Fig. 4. Shape distribution of the rhodoliths from Korytnica and Chomentów.

### Internal structure

The degree of asymmetry as seen in cross section may serve as a measure of immobility, although there is no simple and unequivocal correlation.

Several examples show a structure typical of stable position during the whole period of rhodolith growth, as evidenced by relatively flat base, with no traces of downward growing, and by strongly eccentrically placed nucleus region (pl. 2: 3, 5). This rhodolith type has unusually large voids inside, obviously of primary, constructional origin. Strongly asymmetrical, cne-growth-stage rhodoliths are more frequent in Korytnica than in Chomentów. In other cases, unidirectional growth after ultimate stabiliza-

tion is observed (pl. 2: 2, 6). The very nucleus could hardly be observed in median cross sections, but it is very likely that the earliest stage of rhodolith development takes the form of either small branching thallus or small concentric laminar sphere, until its ultimate immobilization. Sometimes, the asymmetry is inherited from the shape of the nucleus, e.g. bivalve shell or valve (pl. 3: 1, 5).

The second category of rhodoliths comprises forms that show several distinct growth stages, reflecting successive growth positions. In these rhodoliths, strongly asymmetrical, unidirectional growth followed by successive overturnings, led to a more symmetrical form, susceptible to further overturning (fig. 5, pl. 4: 4). As a result, the internal columnar stages are surrounded by rather uniform layer of laminar to columnar thalli documenting more frequent rolling, despite greater dimensions than in the earlier stage.

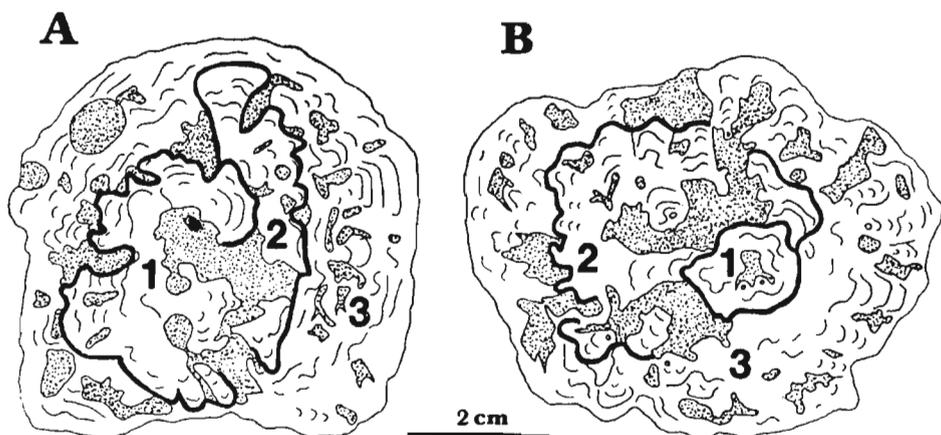


Fig. 5. Internal structure of the multi-stage-growth rhodoliths from Korytnica: A ZPAL AIVI/K3/3; B ZPAL AIVI/K38.

Symmetrical rhodoliths, common in both exposures, show several types of internal structure. Open, branching to columnar forms (pl. 1: 2—3) occur only exceptionally. The majority consist of consecutive or alternating laminar, branching, and columnar thalli (pl. 3: 4, pl. 4: 2, 6) surrounding the nucleus—a fragment of an algal branch, bryozoan colony, some nonpreserved object, or very rarely mollusk shell. Many symmetrical rhodoliths are purely laminar—built of thin thalli devoid of perithallus, or with a strongly reduced one, and with rare conceptacles (pl. 1: 4—5). Their structure is rather regular, concentric. This type is by far more common in Chomentów than in Korytnica.

Two types of growth sequence are most common in Korytnica, viz. branching-columnar/laminar (pl. 2: 5—6, pl. 3: 3), and laminar-branching-columnar (pl. 4: 3—4, 6), whereas purely laminar and laminar-columnar

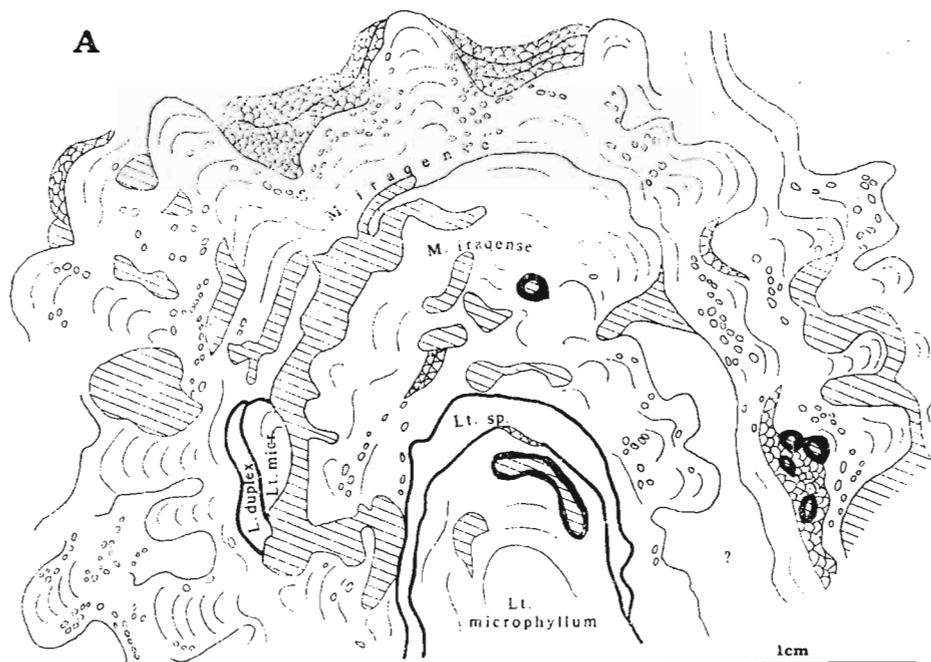
ones are much more rare. The latter two types of rhodolith, i.e. those with exclusive or dominating laminar stage, are much more common in Chomentów than in Korytnica; the growth sequence with initial branching stage is relatively rare in Chomentów, while 3- to 4- stage rhodoliths (laminar-branching-columnar/laminar) are nearly equally numerous in both localities. No particular growth sequence seems to dominate in Chomentów.

### Algal species diversity

Total diversity of the red-algal assemblage that forms rhodoliths is quite remarkable: 26 species of 7 genera. Twenty three species have been found within rhodoliths in Korytnica, while 21 species occur in rhodoliths in Chomentów. This diversity is much higher than that reported from similar facies in Malta (Bosence 1983a) or Spain (Braga and Martin 1988).

There are only four monospecific rhodoliths in the whole analyzed material. All the remaining specimens are multispecific, commonly constructed by 5—8 coralline algal species (fig. 6).

The monospecific rhodoliths show wide-branched growth form, passing externally to columnar growth form. Three of them are built by three distinct species of *Lithothamnion* (*Lt. fruticulosum* (pl. 2: 4), *Lt. ramosissimum*, *Lt. corallinaeforme*), the fourth one represents *Mesophyllum ira-gense*.



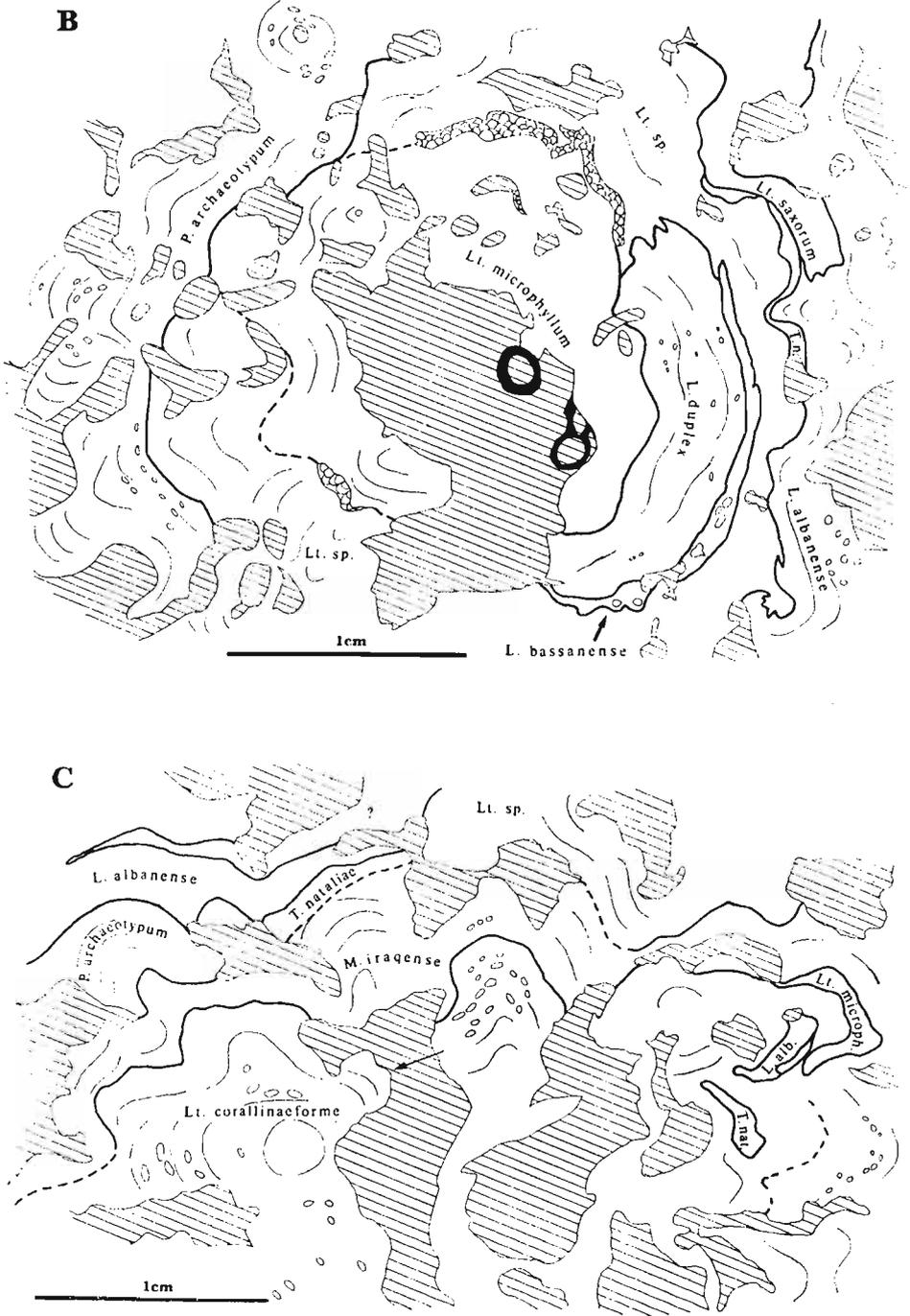


Fig. 6. Internal structure (drawn from a thin section) of the rhodoliths showing distribution and growth forms of algae (blank) and their relations to epibionts (serpulids-black, bryozoans-vesicular) and primary porosity (hachured), Korytnica: A ZPAL A1VI/K36; B ZPAL A1VI/K5/1; C ZPAL A1VI/K2/2.

The multispecific rhodoliths are dominated volumetrically by only a few algal species, the remaining ones being of secondary importance (fig. 6). Four species dominate in Korytnica: *Lithothamnion microphyllum*, *Mesophyllum iraqense*, *Lithophyllum albanense* and ?*Titanoderma duplex*. In Chomentów, the dominant species include additionally *Lithothamnion praefruticosum*, which is present but extremely rare in Korytnica. All these species form massive, thick crusts or crusts with branches, sometimes expanding to columns (fig. 6). In addition, the species *Titanoderma nataliae* shows high frequency in the both localities, though it is volumetrically insignificant due to its very thin thallus.

Two comparisons of specific composition have been made: Korytnica versus Chomentów rhodolith population (fig. 3), and dense versus porous rhodoliths. Among dominant species *M. iraqense* and *T. nataliae* are more frequent in Chomentów than in Korytnica, both being almost equally represented in dense and porous rhodoliths. *Lt. praefruticosum*, dominant only in Chomentów, shows higher frequency in dense rhodoliths. *Lt. microphyllum*, in turn, more frequently dominates in porous specimens.

### Epibionts

Almost all rhodoliths, regardless of their structure, size or density are covered with epibionts: encrusting foraminifers, cyclostomatous and cheilostomatous bryozoans and serpulids (see fig. 6). Indications of competition between the red algae and epizoans are fairly common (pl. 12: 7). No clear difference in density of any of these groups occurs between the two analyzed rhodolith populations, but rhodoliths are generally more heavily encrusted in Chomentów than in Korytnica.

### Borings

Algal, and probably also sponge borings are a striking feature of the investigated rhodoliths (pl. 12: 4, 6). They are often grouped at particular levels within a rhodolith (pl. 12: 6), which reflects episodes of growth cessation of the red algae, the degree of perforation being a function of the duration of exposition. The percentage of rhodoliths with frequent zones of microborings is distinctly higher in Korytnica than in Chomentów. Some rhodoliths reveal also bivalve borings (most probably *Lithophaga*) (pl. 2: 3, pl. 4: 4).

### Thallus thickness

In the greatest part, rhodoliths consist of both thin and thick thalli that overgrow each other or alternate. One type usually dominates, however. Rhodoliths built mainly of thick thalli prevail in both localities

but the percentage of thin-thalli dominated rhodoliths is much greater in Chomentów (see fig. 3). It is not always possible to make the exact specific attribution of these thin thalli, for they consist mainly of hypothallus; in many cases, however, it is evident that they belong to species known from other rhodoliths but with the reduced perithallus and very rare conceptacles.

The high percentage of thin-thalli rhodoliths in Chomentów should have been influenced by environment because thin crusts grow generally faster than thick ones (Steneck 1985).

In summary, the rhodoliths from Korytnica show (see fig. 3), on the average, greater asymmetry, higher primary porosity, less frequent epibionts and more frequent borings. They are built mainly of thick algal thalli, and they are dominated by four algal species of which *Lt. microphyllum* is more frequent than in Chomentów; the prevailing growth sequences include the initial branching stage.

On the other hand, the rhodoliths from Chomentów (see fig. 3) are in general more symmetrical, more massive and bear more frequent epibionts, but borings are less common. The percentage of thin thalli is higher. These rhodoliths are dominated by five species, of which *M. iragense* is more frequent than in Korytnica while *Lt. praefruticosum* is only a subordinate species in this latter locality. The laminar growth form dominates both at early and later stages of rhodolith development in Chomentów.

## Discussion

The observed differences between the two populations of rhodoliths clearly reflect a difference in environmental conditions. The rhodolith features in Chomentów obviously indicate relatively high energy conditions, while those found in Korytnica are typical of more quiet water.

This inference is mainly based on the internal structure of rhodoliths and the dichotomy of massive *versus* porous rhodoliths, i.e. high *versus* low energy, which is widely observed and generally accepted in present day environments (see Bosellini and Ginsburg 1971, Adey and MacIntyre 1973, Minnery *et al.* 1985). It is supported by another dichotomy, viz. thin-laminar, dense, symmetrical rhodoliths *versus* thick-laminar asymmetrical rhodoliths with large constructional voids, reflecting also high and low turbulence, respectively (Bosence and Pedley 1982, Minnery *et al.* 1985). The adaptation of thin thalli to tolerate overturning has been mentioned by Bosence (1983b), who states that coralline-algal crusts with high marginal growth rates are better adapted to substrates that are more frequently turned. A good example of such crusts is provided by many rhodoliths in Chomentów, which are built of thin thalli consisting mainly of laterally growing hypothallus.

The dominance of laminar stages in rhodoliths from Chomentów, as compared to frequently branching stages in specimens from Korytnica, agrees well with the interpretation that refers to differential water energy. The association of branching thalli with quiet water on the one hand, and laminar thalli with turbulent water on the other is now, after extensive studies, rather trivial (see e.g. Bosellini and Ginsburg 1971, Bosence 1976, 1983b).

The absence of a clear dominance of any growth-form sequence in Chomentów raises the question of a possible heterogeneity of the rhodolith population. Some specimens may support this possibility (pl. 4: 5) but the presumed environment of deposition of the coralline-algal limestones from Chomentów, i.e. a small, shallow-water, nearshore carbonate platform (see e.g. Gutowski 1984), seems to rule out the presence of strongly differentiated depositional subenvironments.

The higher frequency of epifauna in Chomentów also supports the inference about shallow-water environment, as Montaggioni (1979) documented more epibionts in turbulent waters of the reef flat and their decrease in quiet water. More important role of microborers in Korytnica, reflecting long period of immobility, agrees well with this interpretation.

The commonly observed alternation of laminar and columnar growth stages (pl. 3: 4) reflects periods of more quiet and more turbulent conditions, respectively (cf. Studencki 1979, 1988a, Bosence and Pedley 1982).

The depth interval separating the inferred zones of sedimentation (i.e. Korytnica and Chomentów zones) was rather moderate, as there is neither a sharp difference in species diversity nor a strong domination of any feature in any locality. The populations differ in frequency relations and not in presence-absence relations, which should be typical of ecologically distant environments. This resembles the observations made by Braga and Martin (1988) in the case of Miocene rhodoliths from southern Spain.

The results of our study confirm the earlier facies and faunistic investigations of Radwański (1969), Bałuk and Radwański (1977) and Gutowski (1984) who referred the difference between the deposits and assemblages of Korytnica and those of Chomentów to the depth differentiation of the basin, where coralline-algal limestones represent more shallow conditions. The synsedimentary tectonic nature of the boundary between these two zones is documented by geophysical studies (Szymanko and Wójcik 1982).

Radwański (1969) postulated extremely shallow-water environment for the sedimentation of coralline-algal limestones in Chomentów, basing this claim on the presence of numerous, extensively bored boulders and pebbles of Jurassic limestones and on general geological considerations. Slightly deeper conditions (ca. 10 meters) have been presumed for the simultaneous sedimentation of Korytnica marly sands with rhodoliths.

## ECOLOGY OF CORALLINE ALGAE

The studies of Recent rhodolith composition in relation to water depth are still at a very beginning, although algal assemblages seem to be rather sensitive to depth, even at the genus level. The investigations in the Gulf of Mexico by Minnery *et al.* (1985) have shown a dramatic change in the generic composition of rhodoliths within an interval of 30 meters. While 8 genera participate in the construction of rhodoliths from the depth range 50—65 m, only two of them are dominant in the next deeper zone (65—80 m). In turn, an increase in species number in rhodoliths from deeper water has been found in the Late Miocene deposits of southern Spain (Braga and Martin 1988).

Although evidently formed under different energy conditions (so probably also at different depths), the rhodoliths from Chomentów and Korytnica do not show a significant difference in composition, even at the species level. Nevertheless, there is a difference, more subtle but distinct. Among the dominant species, *M. iraqense* is more frequent in Chomentów than in Korytnica; *T. nataliae*, volumetrically insignificant but common, is also much more frequent in Chomentów; *Lt. praefruticulosum*, very common and sometimes among dominant species in Chomentów, is practically absent from Korytnica; at last, squamariacean crusts have been found in rhodoliths from Chomentów, while they are absent in Korytnica.

The paleoecological interpretation should also take into account the difference between dominant species in dense *versus* porous rhodoliths. It appears that *M. iraqense* dominates with equal frequency in both types of rhodoliths, while *Lt. microphyllum* is dominant rather in porous rhodoliths which are more stable, not very often overturned. On the other hand, *Lt. praefruticulosum* tends to participate in masive rather than porous rhodoliths, and *T. nataliae* is equally distributed in both types of rhodoliths.

It seems therefore reasonable to assume, that the distribution of coralline algal species has been controlled by two factors: the frequency of overturning or rolling of rhodoliths and water depth (or better depth-related features of the environment). As a result, *M. iraqense* and *T. nataliae*, both equally represented in dense and porous rhodoliths (thus independent of rolling factor), are more common in Chomentów, i.e. in the shallower part of the basin. The anatomical features of the thalli are not against with this interpretation. Thick thalli of *M. iraqense* show either crustose or thick-branched growth-forms, and, in the case of branching thalli, their very numerous conceptacles tend to be concentrated in lateral parts of the branches and near their bases (fig. 6A, pl. 9: 1c, 1d), i.e. in regions well protected against mechanical abrasion and herbivory (Steneck 1985). *T. nataliae*, on the other hand, employed an opposite strategy: its thin crusts are embedded within other thalli, and have rare and raised but probably well sheltered conceptacles.

It is not easy to infer which particular depth-related factor could control the distribution of these two coralline algal species; that is, beyond a rather trivial statement about light requirements.

*Lt. praefruticulosum*, being among the five dominant species in Chomentów but extremely rare in Korytnica, is more common in dense than in porous rhodoliths. This suggests an adaptation to shallow and turbulent waters, although any adaptive features of the kind present in *M. iraqense* are lacking. The preference of *Lt. praefruticulosum* for high energy environment however, is quite well documented in both reefs (Pisera 1985) and rhodoliths (Bosence and Pedley 1982, Studencki 1988a, b).

*Lt. microphyllum* distinctly prefers porous rhodoliths, thus showing low tolerance for rolling.

An attempt have been made to find out whether or not the species within rhodoliths show any succession. Detailed studies have thus far been scarce but various authors tried to show the existence of ecological succession (for short summary see Bosence 1983b). For example, Bosence and Pedley (1982) indicated an ecological succession within Miocene rhodoliths from Malta, with the inner core constructed by *Mesophyllum* and *Lithoporella* and the outer parts by *Lithophyllum*, *Lithothamnion* and *Mesophyllum*. Braga and Martin (1988) in turn have found dominance of crustose to columnar *Lithophyllum viennoti* in a center, followed by branching thalli of *Lt. floreabrassica* and thin *Mesophyllum koritzae*.

No evident regularity in species sequence has been observed within the analyzed material, neither from Chomentów nor from Korytnica, and neither in dense nor in porous rhodoliths. Both the most frequent dominant forms, *M. iraqense* and *Lt. microphyllum*, occur at various stages of rhodolith development, from the inner to outermost parts, forming smooth or mamillate crusts. Thalli of the remaining species also seem to be scattered more or less randomly within particular sequences. Only one species, *Lithophyllum albanense*, tends to avoid the innermost parts, frequently building the outermost parts of rhodoliths.

Although branching thalli generally do not attract borers, some small branching rhodoliths built of *Lithothamnion ramosissimum* show numerous traces of being repeatedly broken or bored, and then regenerated (pl. 12: 5). These observations suggest that this species is highly resistant against damage due to its high growth potential.

#### SYSTEMATIC DESCRIPTION

The name *Lithothamnion* instead of *Lithothamnium* is here adopted, following the generic revision carried by Woelkerling (1983) and accepted by the International Botanical Congress in Berlin in 1987 (Woelkerling, written communication).

*Archaeolithothamnium intermedium* Raineri, 1924

(pl. 5: 3—4)

1965. *Archaeolithothamnium intermedium* Raineri; Johnson: 262, pl. 1: 6.  
 1975. *Archaeolithothamnium intermedium* Raineri; Boulanger et Poignant: 686, pl. 1: 3—4.  
 1983a. *Archaeolithothamnium intermedium* Raineri; Bosence: 150, pl. 15: 3—5.  
 1988b. *Archaeolithothamnium keenani* Howe; Studencki: 17, pl. 3: 1, pl. 9: 5.

*Material.* — 5 thin sections from Korytnica, 2 from Chomentów.

*Description.* — Thalli form free branches or crusts with branches. Hypothallus is in most cases reduced to a thin layer of cells; where better developed, its cells are 20—28  $\mu\text{m}$  long and 10—14  $\mu\text{m}$  wide (20  $\mu\text{m}$   $\times$  10  $\mu\text{m}$  to 28  $\mu\text{m}$   $\times$  14  $\mu\text{m}$ ). Hypothallic cells arranged in ascending filaments but rarely show pseudocoaxial disposition. Perithallus irregularly zoned, with cells arranged in filaments, sometimes in rows. They are 14—22  $\mu\text{m}$  long and 11—14  $\mu\text{m}$  wide (14  $\mu\text{m}$   $\times$  12  $\mu\text{m}$  to 22  $\mu\text{m}$   $\times$  12  $\mu\text{m}$ ). Sporangia grouped at several levels, up to twenty in each group, arranged rather irregularly, oval in section but more or less elongated. They are 100—130  $\mu\text{m}$  high and 50—65  $\mu\text{m}$  wide (100  $\mu\text{m}$   $\times$  60  $\mu\text{m}$  to 130  $\mu\text{m}$   $\times$  50  $\mu\text{m}$ ).

*Remarks.* — The described species is characterized by large, oval sporangia grouped in relatively small clusters, and arranged rather irregularly within clusters. In this respect, the specimens from Korytnica and Chomentów are closely consistent with those from the Miocene of SE France (Boulanger and Poignant 1975) and from the Miocene of Malta (Bosence 1983a).

The specimens from the Pinczów Limestone (Miocene, Poland) previously attributed to *A. keenani* Howe (Studencki 1988b) are entirely consistent with the material under investigation and represent in fact *A. intermedium* Raineri. After comparative investigations of the thalli from the Ukraine, which were distinguished by Maslov (1956) as *A. keenani* var. *lvovicum* (= *A. lvovicum* Maslov of Pisera (1985)), it is clear that they differ from those recorded in Pinczów; their sporangia are smaller on the average, with frequently acute lower and upper tips, grouped in much more numerous clusters, and their perithallic cells are more regularly arranged.

*Occurrence.* — Middle Miocene of Poland (Korytnica Basin, Wójcza-Pinczów Range). Miocene of France, Malta, Libya and Borneo.

*Archaeolithothamnium lvovicum* (Maslov) Pisera, 1985

(pl. 5: 1a—1b)

1988. *Archaeolithothamnium lvovicum* (Maslov) Pisera, 1985; Bakalova: 9, pl. 1: 5—6 (*cum syn.*).

*Material.* — 2 thin sections from Korytnica.

*Description.* — Thalli form crusts, either entirely sterile or with abundant sporangia. Hypothallus most commonly thin, reduced, consisting of small cells (10  $\mu\text{m}$   $\times$  8  $\mu\text{m}$ ) arranged in abruptly ascending filaments, passing into perithallus without sharp boundary. Sometimes, however, hypothallus is fully developed, 120—170  $\mu\text{m}$  thick, consisting of larger cells which are 18—22  $\mu\text{m}$  long and 8  $\mu\text{m}$  wide, arranged either in ascending filaments or in a fan-like manner, passing into perithallus without distinct boundary. Perithallic cells rectangular as a rule, 15—18  $\mu\text{m}$  long and 8—10  $\mu\text{m}$  wide (15  $\mu\text{m}$   $\times$  10  $\mu\text{m}$  to 18  $\mu\text{m}$   $\times$  8  $\mu\text{m}$ ), but sometimes square (8  $\mu\text{m}$   $\times$  8  $\mu\text{m}$  to 10  $\mu\text{m}$   $\times$  10  $\mu\text{m}$ ), arranged in rows, rarely in filaments.

Perithallus shows a distinct, irregular zonation. Sporangia elongated, irregularly oval to hexagonal in section, the oval ones sometimes with acute lower or upper ends, 90–100  $\mu\text{m}$  high and 45–55  $\mu\text{m}$  wide (90  $\mu\text{m}$   $\times$  55  $\mu\text{m}$  to 100  $\mu\text{m}$   $\times$  45  $\mu\text{m}$ ). They are grouped at several levels, up to 65 sporangia in each group. Sporangia in each group are developed from the same row of cells thus giving the impression of their common baseline.

*Remarks.*—The considered specimens are entirely consistent with those from the Ukraine, distinguished by Maslov (1956) as *A. keenani* var. *lvovicum*, then raised, along with the specimens from the Roztocze Hills (Poland), to the species level (Pisera 1985). The shape and disposition of sporangia—oval to pentagonal, in small groups in *A. keenani* Howe, as compared to oval with acute end to hexagonal in *A. lvovicum* (Maslov) Pisera, and the distance, both geographic and stratigraphic, support the distinction between these two species.

Studencki (1988b) included *A. lvovicum* Maslov into the synonymy of *A. keenani* Howe while describing the material from the Pinczów Limestone. His decision is now considered invalid and the specimens from the Pinczów Limestone are here attributed to *A. intermedium* Raineri.

*Occurrence.*—Middle Miocene of Poland (Korytnica Basin, Roztocze Hills, Wójcza-Pinczów Range), the Ukraine and Bulgaria.

### *Archaeolithothamnium* sp.

(pl. 5: 2a–2b)

*Material.*—2 thin sections from Korytnica.

*Description.*—Thallus crustose to columnar, with columns up to 6 mm in diameter and up to 8 mm in length. Hypothallus thin, built of a few rapidly ascending filaments, with cells 16–22  $\mu\text{m}$  long and 11–12  $\mu\text{m}$  wide (18  $\mu\text{m}$   $\times$  11  $\mu\text{m}$  to 12  $\mu\text{m}$   $\times$  22  $\mu\text{m}$ ). Perithallus heavily but irregularly zoned, some zones being much wider and alternating with darker and narrower ones. Cells are 18–22  $\mu\text{m}$  long and 10–13  $\mu\text{m}$  wide (18  $\mu\text{m}$   $\times$  10  $\mu\text{m}$  to 22  $\mu\text{m}$   $\times$  13  $\mu\text{m}$ ) in the dark zones, and 25–30  $\mu\text{m}$  long and 10–14  $\mu\text{m}$  wide (25  $\mu\text{m}$   $\times$  10  $\mu\text{m}$  to 30  $\mu\text{m}$   $\times$  13  $\mu\text{m}$ ) in lighter zones. In both the cases, they are arranged in filaments. Sporangia strongly elongated, fusiform, arranged irregularly and in groups variable in size, 140–160  $\mu\text{m}$  high and 50–65  $\mu\text{m}$  wide (140  $\mu\text{m}$   $\times$  65  $\mu\text{m}$  to 160  $\mu\text{m}$   $\times$  50  $\mu\text{m}$ ).

*Remarks.*—The unusually elongated and large sporangia distinguish the considered species from its congeners. The thalli from Korytnica resemble *A. statiellense* Airoldi, 1932 in its fusiform sporangia, but they are larger and the perithallial cells are longer in the considered species than in *A. statiellense*.

*Occurrence.*—Middle Miocene of Poland (Korytnica Basin).

### *Palaeothamnium archaeotypum* Conti, 1945

1988b. *Palaeothamnium archaeotypum* Conti; Studencki: 19, pl. 3: 6–7 (*cum syn.*).

*Material.*—8 thin sections from Korytnica and 5 from Chomentów.

*Remarks.*—The considered material is consistent with all thalli so far ascribed to this species.

*Occurrence.*—Middle Miocene of Poland (Korytnica Basin, Roztocze Hills, Wójcza-Pinczów Range, northern Carpathian border). Miocene of Austria, Slovakia and France.

*Palaeothamnium kossovense* Maslov, 1962

(pl. 6: 1)

1988b. *Palaeothamnium kossovense* Maslov; Studencki: 19, pl. 3: 2 and 5 (*cum syn.*).*Material.*—5 thin sections from Korytnica and 3 from Chomentów.*Remarks.*—The investigated material is entirely consistent with all the thalli attributed so far to this species.*Occurrence.*—Middle Miocene of Poland (Korytnica Basin, Wójcza-Pinczów Range). Paleocene of the Ukraine (Carpathians) and Italy. Eocene of the Ukraine (Crimea).*Lithothamnion corallinaeforme* Lemoine, 1923

(pl. 6: 3, 4a—4b, pl. 7: 3)

1923. *Lithothamnium corallinaeforme* Lemoine: 276, figs 1—2.1962. *Lithothamnium corallinaeforme* Lemoine; Maslov: 61, pl. 25: 1.*Material.*—3 thin sections from Korytnica and 2 from Chomentów.*Description.*—Massive, compact and dense thalli forming initial crusts from which subsphaerical mamillae expand, growing further into short, apically flattened, closely spaced columns. Columns are 3—5 mm in diameter and 7—8 mm high. Rarely seen hypothallus is 120  $\mu\text{m}$  thick, built of nearly equidimensional cells 12—13  $\mu\text{m}$  long and 10  $\mu\text{m}$  wide, arranged in ascending filaments. Perithallus heavily but irregularly zoned, built of small cells square (10  $\mu\text{m}$   $\times$  10  $\mu\text{m}$ ) or rectangular (10  $\mu\text{m}$   $\times$  7  $\mu\text{m}$  to 12  $\mu\text{m}$   $\times$  9  $\mu\text{m}$ ) in shape, arranged in filaments, locally grid-like arranged. Conceptacles usually infrequent, abundant in only one thallus, large, with thick multiporate roof, 375—720  $\mu\text{m}$  in diameter and 180—300  $\mu\text{m}$  high (375  $\mu\text{m}$   $\times$  180  $\mu\text{m}$  to 720  $\mu\text{m}$   $\times$  300  $\mu\text{m}$ ).*Remarks.*—The original diagnosis of *L. corallinaeforme* given by Lemoine (1923) is incomplete: the investigated thalli were sterile. The unusual morphology of the alga, combined with its small-celled perithallus containing very rare conceptacles, suggests, that the specimens reported by Maslov (1962) from the Ukraine, and those from Chomentów and Korytnica are all conspecific.*Occurrence.*—Middle Miocene of Poland (Korytnica Basin), Miocene of Albania and the Ukraine.*Lithothamnion fruticulosum* (Kützing) Foslie

(pl. 3: 4, pl. 7: 1a—1b)

1919. *Lithothamnium fruticulosum* (Kützing) Foslie; Lemoine: 104, figs 3—4.1988b. "*Lithothamnium*" cf. *fruticulosum* (Kützing) Foslie; Studencki: 22, pl. 5: 3.*Material.*—5 thin sections from Korytnica and 2 from Chomentów.*Description.*—Thalli in the form of crusts with branches or free branching growth. Hypothallus thin, consisting of cells 15—17  $\mu\text{m}$  long and 7—11  $\mu\text{m}$  wide (15  $\mu\text{m}$   $\times$  7  $\mu\text{m}$  to 17  $\mu\text{m}$   $\times$  11  $\mu\text{m}$ ), arranged in rapidly ascending filaments with the basal filament built of longer and narrower cells. Perithallic cells arranged in filaments, 8—12  $\mu\text{m}$  long and 7—9  $\mu\text{m}$  wide (8  $\mu\text{m}$   $\times$  8  $\mu\text{m}$  to 12  $\mu\text{m}$   $\times$  7  $\mu\text{m}$ ). Perithallus densely but irregularly zoned, with frequent lenticular zones resulting from the large number of conceptacles (especially well visible in a section marginal to the

conceptacles). Conceptacles abundant, partly filled with spores, strongly varying both in size and shape. They are most frequently small and ellipsoidal ( $175\ \mu\text{m} \times 100\ \mu\text{m}$  on average) or medium sized and elongated ( $280\ \mu\text{m} \times 125\ \mu\text{m}$  to  $425\ \mu\text{m} \times 110\ \mu\text{m}$ ) but can exceptionally attain  $625\ \mu\text{m}$  in diameter and  $125\ \mu\text{m}$  in height.

*Remarks.*—The large number of conceptacles, their disposition and variability in size and shape closely resemble the figure of this species as given by Lemoine (1923); the similarity concerns also the perithallic features.

*Occurrence.*—Middle Miocene of Poland (Korytnica Basin, Wójcza-Pinczów Range). Quaternary of Sicily. Recent of the Mediterranean Sea, Red Sea and Indian Ocean.

### *Lithothamnion lacroixi* Lemoine, 1917

(pl. 6: 2)

1917. *Lithothamnium lacroixi* Lemoine: 269, figs 17—18.

1988b. "*Lithothamnium*" *lacroixi* Lemoine; Studencki: 23, pl. 6: 5.

non 1962. *Lithothamnium* aff. *lacroixi* Lemoine; Maslov: 63, fig. 38.

non 1985. *Lithothamnium lacroixi* Lemoine; Pisera: 101, pl. 19: 1—2.

non 1988. *Lithothamnium lacroixi* Lemoine; Bakalova: 11, pl. 2: 8.

*Material.*—1 thin section from Korytnica.

*Remarks.*—Traces of falciform spores preserved in several conceptacles clearly indicate the specific attribution of this thallus. Our material deviates from the original diagnosis by Lemoine (1917) solely in greater height of some conceptacles ( $150$ — $170\ \mu\text{m}$  instead of  $110$ — $130\ \mu\text{m}$  observed in most cases).

Examination of the specimens described by Maslov (1962) as *L.* aff. *lacroixi* Lemoine shows that their conceptacles are typical rather of *Mesophyllum*. The same holds also true for the thalli figured by Pisera (1985) and Bakalova (1988), which are provided with high conceptacles filled with 2—3 rows of initial sporangial cells.

*Occurrence.*—Middle Miocene of Poland (Korytnica Basin, Wójcza-Pinczów Range, northern Carpathian border). Miocene(?) of Martinique. Oligocene of Italy.

### *Lithothamnion microphyllum* Maslov, 1956

(pl. 7: 2)

1985. *Lithothamnium microphyllum* Maslov; Pisera: 102, pl. 19: 3—4 (*cum syn.*).

1988b. "*Lithothamnium*" *microphyllum* Maslov; Studencki: 25, pl. 6: 3.

*Material.*—28 thin sections from Korytnica and 22 from Chomentów.

*Remarks.*—This is one of the most common rhodolith builders in the investigated material, easily recognizable by its small conceptacles of characteristic shape and small-celled perithallus. The specimens from Korytnica and Chomentów are entirely consistent with all previously described thalli of this species.

*Occurrence.*—Middle Miocene of Poland (Korytnica Basin, Roztocze Hills, Wójcza-Pinczów Range) and of the Ukraine. Oligocene of Bulgaria and Italy.

### *Lithothamnion praefruticulosum* Maslov, 1956

(pl. 7: 4, pl. 8: 5)

1985. *Lithothamnium praefruticulosum* Maslov; Pisera: 101, pl. 20: 1—3 (*cum syn.*).

1988b. "*Lithothamnium*" *praefruticulosum* Maslov; Studencki: 27, pl. 2: 2; pl. 7: 5.

*Material.*—4 thin sections from Korytnica and 18 from Chomentów.

*Remarks.*—The investigated specimens are entirely consistent with the descriptions and figures referred to in the synonymy.

*Occurrence.*—Middle Miocene of Poland (Korytnica Basin, Roztocze Hills, Wójcza-Pinczów Range, northern Carpathian border). Miocene of the Ukraine and Malta. Oligocene of Italy.

*Lithothamnion prascoi* Mastrorilli, 1967

(pl. 7: 5)

1988b. "*Lithothamnium*" *prascoi* Mastrorilli; Studencki: 27—28, fig. 5 (*cum syn.*).

*Material.*—1 thin section from Korytnica.

*Remarks.*—The thallus from Korytnica is indistinguishable from that figured by Mastrorilli (1967) in its general appearance, shape of the two kinds of conceptacle and cell dimensions. The only difference is in a slightly greater size of the conceptacles:  $190\ \mu\text{m} \times 120\ \mu\text{m}$  to  $280\ \mu\text{m} \times 130\ \mu\text{m}$  in the investigated material as compared to  $150\text{--}220\ \mu\text{m} \times 90\ \mu\text{m}$  in the Italian specimens.

*Occurrence.*—Middle Miocene of Poland (Korytnica Basin, Wójcza-Pinczów Range). Oligocene of Italy.

*Lithothamnion ramosissimum* (Gümbel) Conti, 1945

(pl. 8: 4)

1988b. "*Lithothamnium*" *ramosissimum* (Gümbel) Conti; Studencki: 28, pl. 8: 2 and 4 (*cum syn.*).

1988. *Lithothamnium ramosissimum* (Gümbel) Conti; Bakalova: 13, pl. 3: 6—7.

*Material.*—6 thin sections from Korytnica and 1 from Chomentów.

*Remarks.*—The investigated thalli are consistent with the descriptions and illustrations referred to in the synonymy. They are preserved as fragments of branches that form the nuclei of rhodoliths.

*Occurrence.*—Middle Miocene of Poland (Korytnica Basin, Wójcza-Pinczów Range). Miocene of Austria, Slovakia, France and Iraq. Oligocene of Italy.

*Lithothamnion roveretoi* Airoldi, 1932

(pl. 8: 1a—1b)

1932. *Lithothamnium roveretoi* Airoldi: 66, pl. 10: 1.

1967. *Lithothamnium roveretoi* Airoldi; Mastrorilli: 241, pl. 4: 3—4.

1983. *Lithothamnium roveretoi* Airoldi; Bakalova: 56, pl. 3: 4.

*Material.*—2 thin sections from Korytnica.

*Remarks.*—Hypothallus could not be investigated due to micritization. All the remaining features of the two thalli forming crusts with short mamillae are consistent with the descriptions and illustrations referred to in the synonymy.

*Occurrence.*—Middle Miocene of Poland (Korytnica Basin). Eocene/Oligocene of Bulgaria. Oligocene of Italy.

*Lithothamnium saxorum* Capeder, 1900

(pl. 8: 2)

1988b. "*Lithothamnium*" *saxorum* Capeder; Studencki: 29, pl. 8: 5–6; pl. 13: 7 (cum syn.).

?1988. *Lithothamnium saxorum* Capeder; Bakalova: 13, pl. 5: 8.

*Material.* — 4 thin sections from Korytnica and 7 from Chomentów.

*Remarks.* — Maslov (1956, 1962), Pisera (1985) and Studencki (1988b) reported thalli of *L. saxorum* Capeder provided with subrectangular, relatively low (120–150  $\mu\text{m}$  high on average) conceptacles with flat bottom and undulated roof. On the other hand, Bakalova (1988) figured semilunar conceptacles with regularly arched roof, nearly twice as high as in the specimens from the Ukraine and Poland (214  $\mu\text{m}$  high). This discrepancy needs further studies.

*Occurrence.* — Middle Miocene of Poland (Korytnica Basin, Roztocze Hills, Wójcza-Pinczów Range, northern Carpathian border). Miocene of the Ukraine, Israel, Egypt and Bulgaria(?). Oligocene of Italy.

*Mesophyllum fructiferum* Airoldi, 1932

(pl. 8: 3)

1932. *Mesophyllum fructiferum* Airoldi: 76, fig. 2, pl. 12: 1.

1967. *Mesophyllum fructiferum* Airoldi; Mastroianni: 287, fig. 30, pl. 13: 1–2.

*Material.* — 2 thin sections from Chomentów.

*Description.* — Thalli crustose, relatively thin, commonly 600–800  $\mu\text{m}$  thick. Coaxial hypothallus 200–220  $\mu\text{m}$  thick, with cells not arranged in regular rows, gradually passing into perithallus. Hypothallic cells 15–22  $\mu\text{m}$  long and nearly uniformly 10–11  $\mu\text{m}$  wide. Perithallus irregularly, often lenticularly zoned due to the abundance of conceptacles. Perithallic cells either square (9  $\mu\text{m} \times 9 \mu\text{m}$ ) or rectangular (9–16  $\mu\text{m} \times 8 \mu\text{m}$ ) in shape, arranged in filaments, rarely grid-like. Conceptacles very abundant, filled with 3–4 rows of spores, ellipsoidal to reniform in section, 375–520  $\mu\text{m}$  in diameter, and 190–210  $\mu\text{m}$  high (375  $\mu\text{m} \times 190 \mu\text{m}$  to 520  $\mu\text{m} \times 210 \mu\text{m}$ ).

*Remarks.* — The most distinctive features of the considered thalli, i.e. the conceptacle shape and dimensions as well as the arrangement of hypothallic cells in filaments, correspond well with the original diagnosis of Airoldi (1932) and the later description by Mastroianni (1967). The only difference is in the arrangement of perithallic cells: regular, horizontal rows in the Italian specimens while filaments in the thalli from Chomentów (due to densely spaced conceptacles disorganizing the tissue).

*Occurrence.* — Middle Miocene of Poland (Korytnica Basin). Oligocene of Italy.

*Mesophyllum iraqense* Johnson, 1964

(pl. 9: 1–3)

1964. *Mesophyllum iraqense* Johnson: 480, pl. 1: 5–6; pl. 2: 7.

1975. *Mesophyllum iraqense* Johnson; Edgell and Basson: 176, pl. 5: 4–6.

?1988. *Mesophyllum iraqense* Johnson; Bakalova: 14, pl. 4: 1–2.

1988b. *Mesophyllum* cf. *roveretoi* Conti; Studencki: 35, pl. 2: 1; pl. 12: 1.

*Material.* — 17 thin sections from Korytnica and 22 from Chomentów.

*Supplementary description.* — The species is highly polymorphic. Thalli in the

form of either simple crusts provided with short mamillae, or short massive columns, or long branches. Crustose and columnar growth forms sometimes alternate to form a massive, complex construction. Hypothallus 200  $\mu\text{m}$  thick on the average, consisting of cells 20–32  $\mu\text{m}$  long and 7–11  $\mu\text{m}$  wide (20  $\mu\text{m}$   $\times$  9  $\mu\text{m}$  to 32  $\mu\text{m}$   $\times$  11  $\mu\text{m}$ ), arranged in regular arched rows. Cells of the perithallus and medullary hypothallus 13–18  $\mu\text{m}$  long and 7–10  $\mu\text{m}$  wide (13  $\mu\text{m}$   $\times$  7  $\mu\text{m}$  to 18  $\mu\text{m}$   $\times$  10  $\mu\text{m}$ ), arranged in rows. Thallus strongly but irregularly zoned, with zone boundaries being almost never parallel to each other (pl. 9: 1b–1c). Rows of the perithallic and medullary hypothallic cells oblique to zone boundaries (pl. 9: 1b). Conceptacles very abundant in some cases, but scarce in others; their location in branching and columnar thalli shows a preference to lateral regions (pl. 9: 1c–1d). Conceptacles are variable in shape and size: ellipsoidal, elongated, subrectangular or irregular. They are most commonly 280–350  $\mu\text{m}$  in diameter and 130–170  $\mu\text{m}$  high (280  $\mu\text{m}$   $\times$  130  $\mu\text{m}$  to 350  $\mu\text{m}$   $\times$  170  $\mu\text{m}$ ).

*Remarks.*—The abundant and well preserved material from Korytnica and Chomentów gives an opportunity to recognize the very wide intraspecific variability of *M. iraqense* Johnson and to supplement the species description. It is particularly important to note the change from branching and columnar to crustose growth form. The morphology and internal structure of branches are consistent with the descriptions and figures given by Johnson (1964) and Edgell and Basson (1975).

The holotype presented by Johnson (1964) is sterile; any comparison could thus only refer to its branching nature and its typical irregular zonation. Edgell and Basson (1975) reported several structures they considered to be conceptacles. Recently, Bakalova (1988) figured unquestionable conceptacles, but the general appearance of the branches (very regular cell rows and zones parallel to each other, absence of thick perithallus) resembles neither the specimens from Iraq (Johnson 1964) nor those from Lebanon (Edgell and Basson 1975). Whereas these branches may resemble the thalli of *M. laffittei* Lemoine as figured by Buchbinder (1977), the alleged conceptacles reported by Edgell and Basson (1975) and those presented by Bakalova (1988) are located apically, not laterally in branches.

Some crustose thalli of the investigated species show strong resemblance to *M. roveretoi* Conti (cf. pl. 9: 2–3, Conti 1943, Mastrorilli 1967, Orszag-Sperber and Pognant 1972). Their supposed conspecificity, however, might only be proved by direct comparison to the holotype.

The crustose thalli contributing to rhodoliths in the Pinczów Limestose, assigned previously to *M. cf. roveretoi* Conti (Studencki 1988b), are indistinguishable from the specimens of *M. iraqense* Johnson from Korytnica and Chomentów.

*Occurrence.*—Middle Miocene of Poland (Korytnica Basin, Wójcza-Pinczów Range). Miocene of Iraq, Lebanon and Bulgaria(?).

### *Lithophyllum albanense* Lemoine, 1923

(pl. 10: 4–5)

1988b. *Lithophyllum albanense* Lemoine; Studencki: 36, pl. 2: 1; pl. 12: 2 (*cum syn.*).

1988. *Lithophyllum albanense* Lemoine; Bakalova: 16, pl. 5: 3.

*Material.*—22 thin sections from Korytnica and 13 from Chomentów.

*Remarks.*—The investigated material is entirely consistent with all previously described and illustrated specimens of this species.

*Occurrence.*—Middle Miocene of Poland (Korytnica Basin, Roztocze Hills, Wójcza-Pinczów Range, northern Carpathian border). Miocene of the Ukraine, France, Malta, Algeria, Albania, Bulgaria, Israel and Iraq. Oligocene of Italy.

*Lithophyllum bassanense* Mastrorilli, 1973

(pl. 10: 2a—2b)

1973. *Lithophyllum bassanense* Mastrorilli: 267, pl. 5: 1—2.1988. *Lithophyllum bassanense* Mastrorilli; Bakalova: 16—17, pl. 5: 4.*Material.* — 1 thin section from Korytnica and 1 from Chomentów.*Description.* — Thallus crustose. Hypothallus 130  $\mu\text{m}$  thick, consisting of cells 17—23  $\mu\text{m}$  long and 5—6  $\mu\text{m}$  wide, arranged in regular, arcuate rows. Perithallic cells small, commonly 11  $\mu\text{m}$  long and 7—9  $\mu\text{m}$  wide, arranged in rows, broadly doming the above conceptacles. Zonation rather poorly pronounced. Conceptacles broadly oval, sometimes with flat bottom, provided each with a short, triangular or much longer, rectangular channel. They are 530  $\mu\text{m}$  in diameter and 330—350  $\mu\text{m}$  high; the channel is 170  $\mu\text{m}$  long.*Remarks.* — The considered specimens are consistent with the descriptions and illustrations referred to in the synonymy, except for the size of the conceptacles which are 100 to 200  $\mu\text{m}$  larger in diameter and 100  $\mu\text{m}$  higher than in the holotype.*Occurrence.* — Middle Miocene of Poland (Korytnica Basin). Miocene of Bulgaria. Oligocene of Italy.*Lithophyllum heteromorphum* Mastrorilli, 1967

(pl. 10: 1a—1b)

1967. *Lithophyllum heteromorphum* Mastrorilli: 342, pl. 26: 4—5.1983. *Lithophyllum heteromorphum* Mastrorilli; Bakalova: 61, pl. 5: 1.*Material.* — 2 thin section from Korytnica and 4 from Chomentów.*Description.* — Thallus crustose with short mamillae. Hypothallus very thin, consisting of cells 13—15  $\mu\text{m}$  long and 7  $\mu\text{m}$  wide, arranged in steeply ascending filaments. Perithallic cells arranged grid-like, but sometimes also in filaments. There are two types of uniporate conceptacles: (i) smaller and relatively high conceptacles, 370—470  $\mu\text{m}$  in diameter and 90—130  $\mu\text{m}$  high (370  $\mu\text{m}$   $\times$  130  $\mu\text{m}$  to 470  $\mu\text{m}$   $\times$  90  $\mu\text{m}$ ), and (ii) greater ones, 630—650  $\mu\text{m}$  in diameter and 120  $\mu\text{m}$  high, with triangular channel, typically placed slightly eccentrically. Both the types of conceptacle show in most cases a flat bottom and gently arched roof.*Remarks.* — The two types of hypothallus reported by Mastrorilli (1967), viz. coaxial and noncoaxial, could not be observed in the considered specimens. Nevertheless, the peculiar morphology of conceptacles with eccentric channel and the presence of two distinct size classes of reproductive organs substantiate the specific attribution of the investigated specimens.*Occurrence.* — Middle Miocene of Poland (Korytnica Basin). Oligocene of Italy and Bulgaria.*Lithophyllum ligusticum* Airoldi, 1932

(pl. 11: 2—3)

1932. *Lithophyllum ligusticum* Airoldi: 72, pl. 11: 2—3.1967. *Lithophyllum ligusticum* Airoldi; Mastrorilli: 326, pl. 22: 1—4.part. 1983. *Lithophyllum ligusticum* Airoldi; Bakalova: 62, non pl. 6: 1.*Material.* — 3 thin sections from Korytnica and 1 from Chomentów.

*Remarks.*—The investigated thalli lack hypothallus but the perithallic features and, particularly, the morphology, dimensions, and shape variability of the conceptacles closely fit the descriptions and illustrations given by Airoidi (1932) and Mastrorilli (1967).

The description of *L. ligusticum* Airoidi by Bakalova (1983) is consistent with Airoidi's (1932) diagnosis but the photograph presents a tangential section of a thallus with no characteristic features.

*Occurrence.*—Middle Miocene of Poland (Korytnica Basin). Eocene of Cuba. Oligocene of Italy and Bulgaria.

### *Lithophyllum lithothamnioides* Maslov, 1962

(pl. 11: 1)

1988b. *Lithophyllum lithothamnioides* Maslov; Studencki: 40, pl. 7: 3; pl. 14: 1—2 (*cum syn.*).

*Material.*—1 thin section from Korytnica and 2 from Chomentów.

*Remarks.*—The considered specimens are indistinguishable from those reported by Maslov (1962) and Studencki (1988b).

*Occurrence.*—Middle Miocene of Poland (Korytnica Basin, Wójcza-Pinczów Range) and the Ukraine.

### *Lithophyllum microsporum* Maslov, 1962

1988b. *Lithophyllum microsporum* Maslov; Studencki: 42, fig. 8 (*cum syn.*).

*Material.*—1 thin section from Korytnica.

*Remarks.*—The considered specimen is entirely consistent with the material reported previously; it is not illustrated here because of the poor quality of the thin section.

*Occurrence.*—Middle Miocene of Poland (Korytnica Basin, Wójcza-Pinczów Range). Miocene of the Ukraine, France, Turkey.

### *Lithophyllum cf. perrandoi* Airoidi, 1932

(pl. 10: 3, pl. 11: 4)

*Material.*—3 thin sections from Chomentów.

*Description.*—Thallus crustose with short mamillae growing into branches. Hypothallus regularly coaxial, 120—240  $\mu\text{m}$  thick, consisting of long (26—30  $\mu\text{m}$ ) and narrow (7—9  $\mu\text{m}$ ) cells. Perithallus heterogenous, in places built of smaller cells (11  $\mu\text{m}$   $\times$  7  $\mu\text{m}$ ) in other places consisting of greater cells (16  $\mu\text{m}$   $\times$  7  $\mu\text{m}$ ), arranged in regular rows, with distinct zonation. Conceptacles, generally placed in peripheral parts of the branches, flattened, provided with either broad and triangular or narrow and rectangular channel. They measure 190—250  $\mu\text{m}$  in diameter and 75—95  $\mu\text{m}$  in height.

*Remarks.*—The considered specimens are consistent in conceptacle morphology with those described by Airoidi (1932) and Mastrorilli (1967) as *L. perrandoi* Airoidi although the dimensions given by Airoidi are slightly greater. The main difference is the structure of hypothallus which is regularly coaxial, with distinct row of cells

in the specimens from Chomentów, while indistinctly coaxial, with cells arranged in filaments in the Italian specimens. Also, the perithallic cells are greater and rectangular in the investigated material as compared to small, square cells of *L. perrandoi* Airoldi.

*Occurrence.* — Middle Miocene of Poland (Korytnica Basin).

*Leptolithophyllum platticarpum* (Maslov) Poignant

(pl. 11: 5)

1988b. *Leptolithophyllum platticarpum* (Maslov) Poignant; Studencki: 45, pl. 15: 3 (cum syn.).

*Material.* — 4 thin sections from Korytnica and 3 from Chomentów.

*Remarks.* — The considered specimens are entirely consistent with the specimens referred to in the synonymy.

*Occurrence.* — Middle Miocene of Poland (Korytnica Basin, Wójcza-Pinczów Range). Miocene of the Ukraine and France.

*Titanoderma nataliae* (Maslov, 1956) Studencki, 1988

(pl. 12: 1—2)

1988b. *Titanoderma nataliae* (Maslov) nov comb.; Studencki: 46, fig. 10 (cum syn.).

*Material.* — 18 thin sections from Korytnica and 31 from Chomentów.

*Remarks.* — The considered specimens are entirely consistent with the specimens referred to in the synonymy.

*Occurrence.* — Middle Miocene of Poland (Korytnica Basin, Roztocze Hills, Wójcza-Pinczów Range, northern Carpathian border). Miocene of the Ukraine.

?*Titanoderma duplex* (Maslov, 1962) nov. comb.

(pl. 11: 6—7, pl. 12: 3)

1962. *Lithophyllum duplex* Maslov: 82, fig. 60, pl. 21: 1 and 3.

1971. *Lithophyllum duplex* Maslov; Poignant: 1172, pl. 1.

1972. *Lithophyllum duplex* Maslov; Orszag-Sperber and Poignant: 118.

1977. *Lithophyllum duplex* Maslov; Orszag-Sperber et al.: 290, pl. 4: 4.

1985. *Lithophyllum* cf. *duplex* Maslov; Pisera: 105, pl. 20: 4.

1988b. *Lithophyllum duplex* Maslov; Studencki: 39, pl. 13: 1—2.

non 1988. *Lithophyllum duplex* Maslov; Bakalova: 18, pl. 5: 6.

*Material.* — 18 thin sections from Korytnica and 23 from Chomentów.

*Supplementary description.* — Hypothallus unistratose, consisting of cells obliquely arranged relative to the substrate, 24—44  $\mu\text{m}$  long and 12—15  $\mu\text{m}$  wide (24  $\mu\text{m}$   $\times$  12  $\mu\text{m}$  to 44  $\mu\text{m}$   $\times$  14  $\mu\text{m}$ ). Hypothallic cells directly contact rectangular perithallic cells. Hypothallus is rarely observable.

*Remarks.* — The observations made on the holotype of *Lithophyllum duplex* Maslov have shown that, in the original diagnosis, Maslov (1962) erroneously interpreted the perithallic cells incidentally oriented in arcuate rows near the thallus base as regular, arcuate rows of hypothallus typical of the genus *Lithophyllum*.

In fact, the hypothallus consists of a single layer of oblique cells as described above (pl. 12: 3). This observation has been confirmed on several dozens of thalli in our material and also on thalli from the Roztocze Hills and the Pińczów Limestone. Moreover, the description of *L. duplex* Maslov by Poignant (1971), Orszag-Sperber and Poignant (1972), and Orszag-Sperber *et al.* (1977) give no data on hypothallus except for the statement that it is reduced and difficult to observe.

It is therefore reasonable that *L. duplex* be not attributed to the genus *Lithophyllum* but rather included, due to its unistratose hypothallus, into the genus *Titanoderma* as characterized by Woelkerling *et al.* (1985). The only feature prompting doubts is the perithallus thickness, which is much greater in the species *duplex* than usually reported for the genus *Titanoderma*.

The thalli presented by Bakalova (1988) under the name *L. duplex* Maslov show arcuate arrangement of hypothallic cells and cannot be considered conspecific with the specimens here discussed.

*Occurrence.* — Middle Miocene of Poland (Korytnica Basin, Roztocze Hills, Wólcza-Pińczów Range). Miocene of the Ukraine and France.

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ŚRODKOWOMIOCEŃSKIE RODOLITY Z BASENU KORYTNYCY (POŁUDNIOWA  
POLSKA): ZNACZENIE ŚRODOWISKOWE I PALEONTOLOGIA

*Streszczenie*

W pracy przedstawiono wyniki badań rodolitów pochodzących ze środkowomioceńskich (badeńskich) osadów basenu Korytnicy. Dwie populacje rodolitów, zebrane

z piasków i piaskowców w Korytnicy oraz wapieni glonowych w Chomentowie, wykazują różnice w symetrii, porowatości, dominacji form wzrostowych, oraz subtelne różnice składu gatunkowego glonów je budujących. Rodolity z Korytnicy charakteryzują się większą asymetrią i porowatością, mniej licznymi epibiontami, liczniejszymi wierczeniami i przewagą gruboskorupowych plech. Dominują w nich 4 gatunki: *Lithothamnion microphyllum*, *Mesophyllum iraqense*, *Lithophyllum albannense* i *Titanoderma? duplex*, z których *Lt. microphyllum* występuje częściej niż w Chomentowie. Rodolity z Chomentowa natomiast charakteryzują się większą symetrią, mniejszą porowatością, liczniejszymi epibiontami, rzadszymi wierczeniami oraz przewagą cienkoskorupowych plech. Dominuje w nich 5 gatunków: *Lithothamnion microphyllum*, *Lt. praefruticulosum*, *Mesophyllum iraqense*, *Lithophyllum albannense* i *Titanoderma? duplex*, z których *M. iraqense* występuje częściej niż w Korytnicy.

Różnice powyższe przypisać należy czynnikom środowiska. Obie populacje pochodzą z utworów płytkowodnych, ale cechy rodolitów z Korytnicy wskazują na większą głębokość zbiornika, podczas gdy zespół rodolitów z Chomentowa jest charakterystyczny dla jego płytszej części.

W badanym materiale stwierdzono występowanie 26 gatunków krasnorostów należących do 7 rodzajów (*Archaeolithothamnium*, *Palaeothamnium*, *Lithothamnion*, *Mesophyllum*, *Lithophyllum*, *Leptolithophyllum* i *Titanoderma*). W konstrukcji rodolitów uczestniczy najczęściej 5–8 gatunków, z których 4–5 dominuje objętościowo, a pozostałe mają charakter akcesoryczny. Tylko 4 rodolity z całego badanego materiału okazały się monospecyficzne.

Następstwo gatunków w ponad 100 badanych rodolitach jest czysto przypadkowe i nie wykazuje cech sukcesji ekologicznej.

#### EXPLANATION OF PLATES 1–12

All scale bars 1 cm

#### Plate 1

1. Asymmetrical porous rhodolith, ZPAL AIVI/K33, Korytnica.
2. Symmetrical, porous, branching to columnar rhodolith, ZPAL AIVI/K39, Korytnica.
3. Symmetrical, porous, branching to columnar rhodolith, ZPAL AIVI/K202 (the same specimen as illustrated in Gutowski 1984, pl. 2: 3), Korytnica.
- 4–5. Symmetrical, dense, laminar rhodoliths, Chomentów: 4 ZPAL AIVI/Ch53; 5 ZPAL AIVI/Ch55.

## Plate 2

1. Asymmetrical, dense rhodolith, ZPAL A1VI/Ch59, Chomentów; note eccentrically located (not preserved) nucleus.
2. Asymmetrical, porous rhodolith, displaying unidirectional growth after ultimate stabilization, ZPAL A1VI/K2/, Korytnica.
3. Asymmetrical, one-growth-stage rhodolith with eccentrically situated nucleus (not preserved), ZPAL A1VI/K1/22, Korytnica; note a mollusk boring.
4. Symmetrical, branching, monospecific rhodolith, ZPAL A1VI/K43, Korytnica.
5. Asymmetrical, dense, one-growth-stage rhodolith, ZPAL A1VI/K32, Korytnica.
6. Multi-growth-stage asymmetrical rhodolith (branching-columnar/laminar type of growth) showing unidirectional growth after ultimate stabilization, ZPAL A1VI/K401, Korytnica.

## Plate 3

1. Porous, strongly asymmetrical (asymmetry inherited after shape of nucleus, i.e. bivalve valve) rhodolith displaying columnar growth, ZPAL A1VI/2, Korytnica.
2. Dense, symmetrical rhodolith displaying different types of algal growth, ZPAL A1VI/Ch57, Chomentów.
3. Porous, symmetrical rhodolith with branching-columnar/laminar type of growth, ZPAL A1VI/K1, Korytnica; note a bivalve boring.
4. Symmetrical rhodolith displaying alternation of laminar, branching and columnar thalli, ZPAL A1VI/K38, Korytnica.
5. Asymmetrical rhodolith (asymmetry inherited after bivalve shell, the same specimen as illustrated in Gutowski 1984, pl. 2: 4), showing unidirectional columnar growth after stabilization, ZPAL A1VI/K311, Korytnica.

## Plate 4

1. Dense, asymmetrical rhodolith built of thick crustose to columnar thalli, ZPAL A1VI/Ch201, Chomentów.
2. Symmetrical rhodolith displaying alternating laminar, branching and columnar thalli, ZPAL A1VI/K31, Korytnica.
3. Symmetrical rhodolith displaying laminar-branching-columnar growth, ZPAL A1VI/K41, Korytnica.
4. Multi-stage-growth rhodolith displaying laminar-branching-columnar growth, ZPAL A1VI/K3/3, Korytnica.
5. Two rhodoliths preserved together and displaying different types of growth, ZPAL A1VI/K306, Korytnica.
6. Multi-stage-growth symmetrical rhodolith displaying alternation of laminar, branching and columnar types of algal thalli, ZPAL A1VI/K2/1, Korytnica.

## Plate 5

- 1a—1b. *Archaeolithothamnium lvovicum* (Maslov) Pisera, ZPAL A1VI/Gu2, Korytnica: 1a general view of a columnar thallus with numerous sporangia,  $\times 4$ , 1b details of perithallus with sporangia,  $\times 45$ .
- 2a—2b. *Archaeolithothamnium* sp., ZPAL A1VI/2, Korytnica: 1a  $\times 12$ ; 1b  $\times 55$ .

- 3—4. *Archaeolithothamnium intermedium* Raineri, Korytnica: 3 ZPAL AIVI/K2/7,  $\times 80$ ; 4 ZPAL AIVI/K40,  $\times 40$ .

## Plate 6

1. *Palaeothamnium kossovense* Maslov, ZPAL AIVI/K3/4,  $\times 30$ , Korytnica.
2. *Lithothamnion lacroixi* Lemoine, ZPAL AIVI/K1/22,  $\times 40$ , Korytnica.
- 3—4. *Lithothamnion corallinaeforme* Lemoine: 3 general view of the columnar thallus with characteristic zonation ZPAL AIVI/Ch57,  $\times 20$ , Chomentów; 4a zoned perithallus with multipored conceptacles, ZPAL AIVI/K34,  $\times 40$ , Korytnica; 4b detail of perithallus, ZPAL AIVI/K34,  $\times 80$ , Korytnica.

## Plate 7

- 1a—1b. *Lithothamnion fruticulosum* (Kützing) Foslie, ZPAL AIVI/K43, Korytnica: 1a general view of perithallus with conceptacles,  $\times 40$ , 1b details of perithallus and conceptacles,  $\times 80$ .
2. *Lithothamnion microphyllum* Maslov, ZPAL AIVI/K2/2,  $\times 75$ , Korytnica.
3. *Lithothamnion corallinaeforme* Lemoine, ZPAL AIVI/Ch8,  $\times 20$ , Chomentów.
4. *Lithothamnion praefruticulosum* Maslov, perithallus with multipored conceptacles, ZPAL AIVI/K38,  $\times 40$ , Korytnica.
5. *Lithothamnion prascoi* Mastroianni, ZPAL AIVI/K4/25,  $\times 40$ , Korytnica.

## Plate 8

- 1a—1b. *Lithothamnion roveretoi* Airoidi, ZPAL AIVI/K2/2, Korytnica: 1a general view of perithallus with conceptacles,  $\times 40$ ; 1b details of conceptacles and perithallus,  $\times 80$ .
2. *Lithothamnion saxorum* Capeder ZPAL AIVI/K5/1,  $\times 75$ , Korytnica.
3. *Mesophyllum fructiferum* Airoidi, ZPAL AIVI/Ch8,  $\times 40$ , Chomentów.
4. *Lithothamnion ramosissimum* (Gümbel) Conti, ZPAL AIVI/K1/3,  $\times 80$ , Korytnica.
5. *Lithothamnion praefruticulosum* Maslov, thallus with strongly elongated multipored conceptacles, ZPAL AIVI/K33,  $\times 40$ , Korytnica.

## Plate 9

- 1—3. *Mesophyllum iraqense* Johnson, different aspects of polymorphic species: 1 ZPAL AIVI/K36, Korytnica; 1a fragment of a branch with irregularly zoned perithallus,  $\times 40$ , 1b hypothallus and irregularly zoned perithallus,  $\times 50$ , Korytnica; 1c—1d thalli with conceptacles concentrated near the base and in lateral parts of a branch,  $\times 20$ ; 1e crustose thallus,  $\times 20$ ; 2 crustose zoned thalli with multipored conceptacles, ZPAL AIVI/39,  $\times 80$ , Korytnica; 3 details of a crust with coaxial hypothallus and multipored conceptacles, ZPAL AIVI/K31,  $\times 40$ , Korytnica.

## Plate 10

- 1a—1b. *Lithophyllum heteromorphum* Mastrorilli, ZPAL AIVI/K33, Korytnica: 1a  $\times 40$ ; 1b  $\times 80$ .
- 2a—2b. *Lithophyllum bassanense* Mastrorilli, ZPAL AIVI/K5/1, Korytnica: 2a crustose thallus with conceptacles,  $\times 30$ ; 2b details of thallus with coaxial hypothallus and unipored conceptacle,  $\times 75$ .
3. *Lithophyllum* cf. *perrandoi* Airoldi, ZPAL AIVI/Ch1,  $\times 35$ , Chomentów.
- 4—5. *Lithophyllum albanense* Lemoine, Korytnica: 4 perithallus with conceptacles, ZPAL AIVI/K1/22,  $\times 75$ ; 5 poorly coaxial hypothallus, ZPAL AIVI/K3/4,  $\times 75$ .

## Plate 11

1. *Lithophyllum lithothamnioides* Maslov ZPAL AIVI/K1/22, Korytnica,  $\times 80$ ; note that uniporate conceptacles is developed directly on the hypothallus and within very thin perithallus.
- 2—3. *Lithophyllum ligusticum* Airoldi, Korytnica: 2 ZPAL AIVI/K4/26,  $\times 30$ ; 3 ZPAL AIVI/K1/22,  $\times 75$ .
4. *Lithophyllum* cf. *perrandoi* Airoldi ZPAL AIVI/Ch55,  $\times 40$ , Chomentów; perithallus with characteristic conceptacles.
5. *Leptolithophyllum platticarpum* (Maslov) Pognant, ZPAL AIVI/2,  $\times 40$ , Korytnica.
- 6—7. *Titanoderma? duplex* (Maslov) nov. comb., Korytnica: 6 ZPAL AIVI/K39,  $\times 80$ ; 7 ZPAL AIVI/K1/3,  $\times 30$ .

## Plate 12

- 1a—1b. *Titanoderma nataliae* (Maslov) Studencki, ZPAL AIVI/K1/22, Korytnica: 1a sterile thallus,  $\times 75$ ; 1b thallus with unipored conceptacle,  $\times 75$ .
2. *Titanoderma nataliae* (Maslov) Studencki, thallus with unipored conceptacle, ZPAL AIVI/K1/3,  $\times 75$ , Korytnica.
3. *Titanoderma? duplex* (Maslov) nov. comb., perithallus and unistratose hypothallus consisting of obliquely arranged cells, ZPAL AIVI/K301,  $\times 75$ , Korytnica.
4. Algal borings in an algal thallus, ZPAL AIVI/K34,  $\times 20$ , Korytnica.
5. Damaged and repaired thallus of *Lithothamnion ramosissimum* (Gümbel) Conti, ZPAL AIVI/K45,  $\times 15$ , Korytnica.
6. A level of ?sponge borings in a branch of *Mesophyllum iraqense* Johnson, ZPAL AIVI/K41,  $\times 20$ , Korytnica.
7. Interior of a small rhodolith built of competing algal thalli (black) and bryozoans (AIVI/Gu2),  $\times 6$ , Korytnica.

