Fossilization processes of the microbial mat developing in clastic sediments of the Puck Bay (southern Baltic Sea, Poland)

ABSTRACT: The modern microbial mat from clastic deposits of the Puck Bay coastal shallows and Holocene siliciclastic, laminated deposits were studied by means of sedimentological and geomicrobiological methods. It was discovered that the latter one originated as a result of burial of microbial mats. This is indicated by structural features of the deposits (i.e. relatively high organic matter content, lamination) and by species composition of microfossils of which cyanobacteria, green algae and diatoms are the most abundant. Amongst cyanobacteria there both coccoid and filamentous forms occurred. Filamentous forms were represented by genera Lyngbya, Oscillatoria, Phormidium and Spirulina. These are the main mat-forming microorganisms during the summer bloom of cyanobacteria (late August – early September). The predomination of Opephora olsenii amongst diatoms and relatively high content of filamentous cyanobacteria indicate that Holocene laminated deposits originated as a result of fossilization of microbial mats at their maximum development i.e. during the bloom of cyanobacteria. At that time the Puck Bay mat possesses the highest preservation potential. This is favored by high organic matter content, elimination of zoobenthos, low activity of hydrodynamic factors and rapid burial of the mat by the sediments. The origin of Holocene laminated deposits is connected with the Puck Bay water level rise during the last millennium.

INTRODUCTION

In the middle of 1970’s there began a period of growing interest in studying microbial mats considered as modern analogs of ancient stromatolites. Because of the occurrence of stromatolites in carbonaceous deposits, particularly originated in hypersaline environments, mats from modern counterparts of these environments attracted great concern of sedimentologists and geomic-
robiologists (e.g., WALTER 1976, COHEN & al. 1977, HORODYSKI & al. 1977, Krumbein & COHEN 1977, Krumbein & al. 1977, AWRAMIK & al. 1978). Despite the fact that sporadically stromatolites were also encountered in clastic rocks (DAVIS 1968) amongst sedimentologists there exists the opinion that microbial mats developing in clastic sediments can not be preserved in the fossil state.

The doubts concerning the survival of microbial mats of clastic sediments in fossil state induced the Author to undertake the studies which are reported in the present paper. In the period of 1984—1988 in the Puck Bay coastal zone (southern Baltic Sea, Poland) there were carried out studies of modern microbial mats developing in clastic sediments and of biogenic laminated deposits, which are thought to be potential, siliciclastic stromatolites. Detailed studies aiming to determine the genetic relationship between the mat and the Holocene laminated deposits were begun in 1984. Macroscopic analysis of the organic matter of the latter revealed its composition to be of very fine detritus with little amount of higher plant remnants. Moreover, structural features, i.e. mutually intercalating organic and mineral lamines, pointed out similarities of the aforementioned deposits to the modern stromatolites of Solar Lake, Israel (KRUMBEIN & COHEN 1977).

In order to explain the origin of the biogenic laminated deposit of the Puck Bay coastal zone there was devised research programme which included:

(i) sedimentological characteristics of the deposits;
(ii) species composition of microorganisms of modern microbial mat and of laminated deposits including paleoecological analysis;
(iii) biomarker analysis in order to detect sources of organic matter deposited in these sediments (see MALIŃSKI & al. 1988);
(iv) comparison of the research results of microbial mat and of Holocene laminated deposits with those of fossil laminated deposits.

The working hypothesis accepted at the beginning assumed that biogenic laminated deposits originated as a result of the mat burial by the sediment transported from nearby deeper part of the Puck Bay. For verifying this assumption, the sediment and the microphytobenthos samples of the aforementioned area were analyzed as well.

Affirmative results of the studies of the deposits of the North Sea tidal flats (REINECK 1979; GERDES & al. 1984a, b) and of laminated deposits of the Puck Bay (WITKOWSKI & Krumbein 1986) encouraged the Author to undertake attempt in finding fossil siliciclastic deposits of microbial origin. For this purpose there were chosen laminated, finegrained sandstones of Lower Jurassic (Liassic) of the northern margin of the Holy Cross Mts, Central Poland. It was discovered that these deposits might have originated from the fossilization of the microbial mats (WITKOWSKI, in preparation).

DESCRIPTION OF THE STUDY AREA

The Puck Bay basin is situated in the western part of the Gdańsk Bay and is sheltered between sandy barriers of Hel Peninsula and Gull Reef. The study area encompassed the shore zone of the Hel Peninsula and the neighboring
Fig. 1. Location of the study area in the Puck Bay
1 — Location of the studied profiles, denoted as A, B and C; 2 — Sampling site of the deposits in the central part of the Puck Bay; 3 — Isobaths in metres; 4 — Biogenic laminated deposits; 5 — Medium and fine sand; 6 — Coarse sand with an admixture of gravel; 7 — Silty sand; 8 — Sandy silt; 9 — Fine detrital peat; 10 — Coarse detrital peat including a rhizome level
part of the coastal shallows (Text-fig. 1). The Puck Bay with an area of 104.3
km² (NOWACKI 1980) has a little differentiated, nearly flat bottom. Its maximum
depth is 9.4 m (average 3.0 m). The most characteristic feature of the bottom
relief of the Puck Bay is the presence of extensive coastal shallows (see
FILIPOWICZ 1982).

The water body of the bay with a salinity approaching 8‰ represents
a brackish-water (mixomesohaline) environment. The occurrence of submerged
Gull Reef barrier limits the water exchange between the Puck Bay and the
Gdańsk Bay and significantly affects waves processes in the study area. Because
of small size and natural barriers there originate only local waves of wind
origin. SZOPOWSKI (1961) found out that in the area of Kuźnica the maximum
height of surf waves attains 50 cm. The frequency of waves with the specified
height given by SZOPOWSKI indicates that for 88.6% of the year there are no
waves (17.3% of this is caused by the ice cover). The water level changes in the
the Puck Bay area depend on winds of local origin and these acting over the
whole Baltic Sea. The Puck Bay water level raises with WSW — N — ENE
winds and falls down with winds from other directions. The range of these
changes is from ca. 10 to about 50 cm, maximum up to 170 cm (STOMIANKO
& al. 1974, NOWACKI 1980). The rate of the bay water level changes is variable;
it happens that the rise or decrease of water level of significant range occur
within only several hours (NOWACKI 1980). During the fieldwork, changes up to
20 cm were noticed within 2—3 hours. These lower or raised water levels in the
study area remain for at least several days (Text-fig. 2).

![Figure 2: Short-term changes of the Puck Bay water level (after NOWACKI 1980)](image)

Fig. 2. Short-term changes of the Puck Bay water level (after NOWACKI 1980)
FOSSILIZATION PROCESSES

The influence of the water level changes on the hydrodynamic regime of the bay is most pronounced in the zone of coastal shallows. Because of the flat bottom of this zone even an insignificant decrease of the water level uncovers a belt of sediment ranging in width from several tenths to a few hundred of meters (Pl. 1).

The predominating sediment type of the Puck Bay is sand. The finest, silty sands cover the bottom within a depth range of 2.0—3.0 m, close to the village of Swarzewo and the mouth of the Reda river. In the zone of coastal shallows where the study area was located and in central part of the bay there occur fine- and mediumgrained sands, which are very well and well sorted (WITKOWSKI & MUSIELAK 1982, MUSIELAK 1984). In the northern part of the bay (southward of the study area) where the water depth approaches 2.0 m, fine sands occur. These are moderately well sorted (δ1 changes from 0.59 to 0.79) sediments with mediane (Md) values ranging from 0.19 to 0.21 mm. In the coastal zone westward from Kuznica mediumgrained sands of Md values 0.35 to 0.40 occur. This is well and moderately well sorted sediment with δ1 values from 0.47 to 0.60. Eastward of the aforementioned point, coarsegrained sands with an admixture of gravel are recorded.

METHODS OF STUDY

Samples for determination of species composition of mat-forming microorganisms were taken into test tubes by spatula on average once a quarter. The biogenic laminated deposits were sampled from ditches dug up beyond the extent of water. Depending on their destination, samples were taken into sterile test tubes, jars or as fragments of solid onto aluminium foil.

For granulometric analysis there were chosen 15 samples of modern mat and 20 of biogenic laminated deposits. Prior to the analysis organic matter was removed by combustion in a 550°C for 5 hours. On the basis of the granulometric analyses results, mediane (Md) was determined and subsequently standard deviation (δ1), graphic skewness (SKD) and curtosis (KD) according to formulas of FALK and WARD were counted.

The mineralogical composition of the deposits was determined in thin sections and by means of X-ray diffractography. Thin sections of microbial mat and biogenic laminated deposits were prepared after their solidification with resin.

Samples for cultivation of phototrophic microorganisms of the biogenic laminated deposits of ca. 2.0 g were taken in the field into sterile test tubes and transferred to laboratory poured with ca. 10 ml of double concentrated Allen medium. Samples were cultivated in room temperature under light.

The species composition of cyanobacteria and green algae occurring in the modern microbial mat was determined in water preparations. Whereas diatoms were identified in solid preparations, which were made after removing organic matter by boiling samples in 30% H2O2. Permanent diatom preparations were mounted using Naphrax. Diatoms were identified by means of light microscope equipped with phase contrast under the objective 100 × using an immersion oil. In each sample 300 to 500 frustrules were counted. Moreover for chosen samples there the differentiation index (H') was calculated.

The species composition of microfossils occurring in Holocene laminated deposits was determined in several different ways.

Cyanobacteria and green algae from incubated samples were identified in water preparations. Diatoms were identified in solid Naphrax preparations. According to method recommended by CRONBERG (1986) there were identified cyanobacteria and green algae. In this method the
amorphous organic matter is removed by 10% NaOH solution treatment. The precleaned remnants of microorganisms are fuchsine-B stained and analyzed under the light microscope.

The occurrence of microfossils in the Holocene laminated deposits was also examined in thin sections and under the scanning electron microscope (SEM). The SEM preparations spurred with gold were observed under the Tesla BP 3002 scanning microscope.

DESCRIPTION OF THE DEPOSITS

Studies of the biogenic laminated deposits and of underlying peat were performed in three profiles (denoted in Text-fig. 1 as A, B, and C). These deposits occur along the Hel Peninsula between Władysławowo and Jurata. Because of greater resistance to the destructive wave action laminated deposits form a kind of microcliff ca. 50 cm high. The sole part of these deposits occur at the height of the Puck Bay average water level. Outcrops of laminated deposits are easily detected at the Hel Peninsula maps; in areas of their occurrence the peninsula is much broader (Text-fig. 1).

The best developed profile of biogenic laminated deposits occurs at Władysławowo (profile A). Total thickness of the investigated deposits reaches in this profile 1.0 m. In the lower part of the profile there occurs 50 cm thick layer of peat. In the sole of this layer there was recorded a presence of ca. 30 cm of coarse detrital peat, including a well preserved level of rhizomes of peatforming vegetation. However, above ca. 20 cm of fine detrital peat occurs. In the upper part of the profile A, biogenic, siliciclastic laminated deposits of ca. 50 cm in thickness occur. In the sole of laminated deposits a layer of silty sand of ca. 2 cm in thickness occurs. The contact between silty sand and underlying peat is of erosional origin. Similarly developed deposits were recorded in profile B, which is located within the beach at the open Baltic Sea near Chalupy. The differences denoted here are mainly concerning thickness of the appropriate layers. Total thickness of the investigated deposits in this profile attained 50 cm. In the sole part of profile B, however, one finds a layer of peat only a few centimeters thick with a well preserved in situ rhizomes level. Above this peat layer an intercalation of laminated deposits 10 cm thick occurs. In the upper part of profile B a 20 cm thick peat layer was noted. In the uppermost part of the latter, poorly developed lamination was distinguished. The characteristic feature of this peat was a high mineral detritus content, ranging from 44.7 to 78.8%. The third of investigated profiles occurring at Chalupy (denoted as C) was devoid of peat. There, only the presence of laminated deposits intercalated with a layer of coarse sand including an admixture of gravel was recorded. Total thickness of these deposits amounts ca. 40 cm (Text-fig. 1).

The radiometric age of the studied deposits was determined by means of \textsuperscript{14}C method. The subject of the radiometric studies were peats from profiles A and B. The sole part of the peat in profile A indicated age of 2098 ± 34 y B.P., while the upper one of 789 ± 132 y B.P. Whereas those of profile B studied by MUSIELAK (1989) showed 900 ± 100 y B.P. and 320 ± 100 y B.P. in the sole and upper parts respectively. The occurrence of the laminated deposits in the profile A (above the dated peat) and in the profile B (underneath the dated peat) suggests that the deposition of the laminated sediments began in the Puck Bay area coastal shallows in XI—XIIth century. This idea is supported by other events which took place in this area around that time. Namely between the VIth and XIIth century in Puck there existed a medieval harbour. Nowadays the harbour construction is ca. 1.0 m below the modern Puck Bay water level. The time of its submergence was determined to fall in the XI—XIIth centuries (ZBIERSKI 1988).
The most characteristic feature of the investigated deposits is the presence of lamination. It is displayed as mutual intercalations of sandy and organic laminae (Pl. 2). Thickness of particular laminae is variable and changes from 0.5 to 2.0 cm and from 0.5 to 5.0 cm for organic and mineral ones respectively. The horizontal extent of particular lamines is fairly big, their wedging out is rarely to be seen. Both sole and upper surfaces of lamines are uneven, though they are of the same shape. In the lower part of the profile silty intercalations occur. Their horizontal extent varies from more than 10 to less than 100 cm.

The total organic matter content of laminated deposits changes from 4.0 to 15.0% (Chalupy, profile C) and from 4.0 to 21.0% (Wladyslawowo, profile A). Sandy laminae are nearly exclusively composed of mineral detritus, with a neglectible organic matter content. Whereas in organic laminae besides the organic matrix, variable amounts of mineral fraction are recorded. The organic matter of biogenic laminated deposits occurs in two forms, firstly as remnants of microorganisms (microfossils), macroalgae, fungi and higher plants; and secondly as amorphous products of biodegradation of both micro- and macrophytes. It was estimated on the basis of NaOH solution extraction that amorphous components prevail in the organic layers.

Granulometric analysis indicated that laminated deposits are composed of mediumgrained sands with an admixture of fine ones. Their medians values change from 0.33 to 0.37 mm. The content of gravel fraction amounted less than 1.0%, whereas of fraction below 0.063 mm was variable and ranged from 1.3 to 7.9%. The percent content of the latter tended to raise in the lower part of the profile. The analysis of graphic coefficients i.e. standard deviation, graphic skewness and curtosis revealed textural similarity of mineral detritus of the laminated deposits. The standard deviation values indicated that sorting of the sediments changes from moderately well ($\delta_1 = 0.58—0.62$) to moderately sorted ($\delta_1 = 0.93—1.12$). In all of the samples studied the graphic skewness values were positive and ranged from 0.08 to 0.53. Also the $K_g$ values change within a small range, from 1.05 to 2.0; this means that the frequency curves are steep (WITKOWSKI 1989).

From the analyses of thin sections and X-ray diffractogrammes of the laminated deposits it was inferred that quartz is the main sedimentforming mineral. In all diffractogrammes analyzed, there predominated reflections indicating the presence of quartz. Moreover, as minor components there were recorded feldspars (microcline), clay minerals (kaolinite, illite and smectite) and muscovite (Text-fig. 3). The mineral composition of the investigated deposits changes in vertical profile. In the upper part of the profile, the mineral detritus is nearly exclusively composed of quartz. There only single reflections of feldspars are recognized. Only in samples from the depth

![Fig. 3. Diffractogramme of Holocene biogenic laminated deposits (profile A, depth 20 cm: organic layer)](image)
below 20 cm, do more frequent reflections of clay minerals and muscovite appear. Their presence can be partly connected with intercalations of the very fine sediment occurring in this part of the profile and partly with diagenetic processes. During summer and early autumn (June — October) the outcrops surface becomes covered with the white coating, which according to X-ray diffractography is composed of gypsum. It is only present inside organic laminae and forms rosettes of several dozens of micrometers in diameter. Despite relative high iron content, approaching 60 mg per gram of dry sediment, in the biogenic laminated deposits no pyrite presence was detected. In the thin sections analyzed, however, plant remnants incrustled with ferric oxide were recorded.

The granulometric analysis of modern microbial mat revealed that these are mediumgrained sands with median values changing from 0.35 to 0.40 mm. In none of the samples analyzed was an admixture of gravel detected. The comparison of the mat granulometric composition in different stages of its development shows the relationship between the mineral detritus granulation and the organic matter content. In spring samples of microbial mat the organic matter content is lower than 1.0% and the share of fraction below 0.063 mm amounts less than 0.5%. The content of the latter significantly increases (in average up to more than 10.0%) in mat sediments during the summer bloom of cyanobacteria, i.e. generally with organic matter content rise. The share of organic matter content at that time approaches 50.0%. Another mechanism of mat enrichment with the fraction below 0.063 mm is sedimentation of mineral suspension in water, which persisted in bottom depressions during periods of the Puck Bay water level decrease. The values of standard deviation indicate that microbial mat sediments of spring time, when the organic matter content is low, are well ($\delta_1 = 0.47$) and moderately well ($\delta_1 = 0.60$) sorted. Along with the organic matter content rise, the mat sediments become worse sorted. The graphic skewness attained in analyzed samples both positive and negative values. They changed within a narrow range, from $-0.36$ to 0.13. Similarly curtosis values changed insignificantly, from 1.0 to 1.5.

The mineral composition of microbial mat deposits is strongly dominated by quartz. This was inferred from both thin sections and X-ray diffractography analyses. As minor components feldspars, kaolinite and illite occurred.

MODERN MICROBIAL MAT

In the superficial layer of the bottom sediments of the Puck Bay coastal shallows zone during the vegetation season microphytobenthos develops intensely. As a result of the sediment colonization the microbial mat is formed. The sediment particles are bound both by overgrowing them microorganisms and excreted by microbes mucilaginous sheaths as well as by products of degradation of living in the sediment microphytes (see Pl. 3). The mat forming microorganisms consolidate the sediment surface, protecting it against the destroying influence of waves and currents. In the area of microbial mat occurrence, the rhythmic sediment transport forms, i.e. ripplemarks, did not occur even in the surf zone (see Pl. 1). The only suitable ground for the mat development in the Puck Bay area are fine- and mediumgrained sands. The lateral extent of microbial mat in the studied area is only restricted to the aforementioned sediment types. From observations realized in the period of 1977-78 it is indicated that microbial mat does not develop in the zone of coarse sand occurrence, which is influenced by waves and currents penetrating from the Gdańsk Bay (WITKOWSKI & MUSIELAK 1982).

The mat microecosystem is composed of cyanobacteria, green algae, diatoms, chemoautotrophic bacteria (Beggiatoales), sulfur fotosynthetic bac-
The Puck Bay coastal shallows during the period of water level decrease

A — Microbial mat exposed in the surf zone; August 1984

B — Puck Bay littoral zone exposed at the considerable water level decrease, arrow points out the buried microbial mat (photograph courtesy of Dr. S. Rudowski)
FOSSILIZATION PROCESSES

...teria (Chromaticaceae), chemoheterotrophic bacteria and euglenophytes, occurring occasionally but in masses. Amongst them cyanobacteria, green algae and diatoms are the most important mat builders. Their distribution in the mat environment indicates seasonal differentiations. During spring mostly green algae and diatoms predominate. The increase of cyanobacteria content begins early in summer. The mass occurrence of euglenophytes coincided with the summer bloom of cyanobacteria. More detailed information concerning the species composition of the microbial mat studied is given elsewhere (Witkowski, submitted).

In the microbial mat community 39 species of coccoid and filamentous cyanobacteria were found, 15 of which were of coccoid and 34 of filamentous forms (see Pl. 3). The coccoid forms were almost exclusively represented by the order of Chroococcales. Amongst them most frequently recorded were Microcystis aeruginosa, M. reinboldii, Merismopedia glauca, M. punctata, Chroococcus minutus, Ch. turgidus, and Aphanothece castagnei. Coccoid cyanobacteria occur both at the sediment surface (particularly on sediment uncovered with water) and within the sediment. Their aggregates comprise significant amounts of fine mineral detritus. Coccoid forms dominate amongst cyanobacteria of spring time.

Filamentous forms appear in the microphytobenthic community somewhat later and they attain their maximum development during the summer bloom of cyanobacteria. They are represented by the Oscillatoriales and Nostocales with Oscillatoriales strongly predominating. At first appear Oscillatoria chalybea, O. limnetica, O. tenuis and Pseudanabaena catenata followed later by e. g. Oscillatoria margaritifera, Lyngbya aestuarii, Phormidium fragile, Ph. tenue, Spirulina baltica, and S. subsalsa. However, only in late August and early September do the filamentous forms occur in masses. There occurred far less frequently planktic cyanobacteria of the Nostocales e. g. Anabaena flos-aquae, A. torulosa, A. variabilis, Aphanizomenon flos-aquae, and Nodularia spumigena. Except for the summer cyanobacterial bloom, filamentous forms are an insignificant component of the microbial mat.

Green algae are represented by members of the families Phytomonadales, Chlorococcales and Ulotrichales. The most abundant were unicellular representatives of the Chlorococcales. Amongst these Scenedesmus quadricauda, S. ecernis, S. dispar and Monoraphidium contortum predominated. Less frequently occurred Scenedesmus acuminatus, S. acutus, S. opoliensis, Pediasstrum boryanum, P. integrum, and P. praecox. These algae occur in the uppermost sediment layer throughout the growing season, though their abundance is highest during spring. The Phytomonadales were represented by specimens of the genera Chlamydomonas and Pandorina, but Chlamydomonas sp. was mainly observed during spring. Single specimens of Pandorina sp. were noted in samples collected during the summer bloom of cyanobacteria. The ulotrichales belonged to the algae represented by small amounts of specimens but they were permanent compounds of the microbial mat. There were identified Stichococcus bacillaris and Ulothrix sp.
With respect to the number of species and amount of specimens, diatoms are the most differentiated group of mat forming microorganisms. On the basis of species composition and community differentiation analyses amongst mat diatoms two groups were distinguished:

- diatoms typical of the microbial mat environment,
- diatoms typical of the Puck Bay interior "lagoonary".

The affiliation of given diatom taxon to the particular group was determined according to the following criteria: frequency of occurrence in the mat environment, number of specimens, the ratio between number of alive specimens and empty frustules of given taxon. There also the ratio of whole to crushed frustules was considered as indicator of diatom redeposition.

To the group of diatoms typical of mat environment following taxa are included: *Achnanthes delicatula*, *Cocconeis placentula*, *Fragilaria construens* v. *venter*, *F. virescens* v. *subsalina*, *Navicula cryptolyra*, *N. protracta*, *N. salinarum*, *Nitzschia fonticola*, *Opephora olsenii*, *Synedra pulchella*, and *S. tabulata* (see Pl. 4). The characteristic feature of this group is insignificant detritus content. Amongst them the most common and abundant are *A. delicatula*, *F. construens* v. *venter*, *F. virescens* v. *subsalina*, *N. cryptolyra*, and *O. olsenii*. The total percent content of this group in the composition of the mat diatom community varies from 70 to over 90%. The percent content of two dominating forms *A. delicatula* and *O. olsenii* is subject to significant seasonal changes. The highest percentages of *O. olsenii* (up to 41%) were recorded during the summer bloom of cyanobacteria, while the highest percentages of *A. delicatula* (up to 52%) appeared throughout the rest of the vegetation season. In samples with *A. delicatula* dominance the lowest *O. olsenii* contents (less than 20%) were noted. Diatoms typical of the microbial mat environment are mainly brackish-water forms. Indifferent and halofilous (fresh-water) ones i.e. *Cocconeis placentula*, *Fragilaria construens* v. *venter*, *F. virescens* v. *subsalina*, and *Navicula protracta* occurred less frequently.

Diatoms typical of the deeper part of the Puck Bay were represented by a large group of taxa recorded as single specimens. The characteristic feature of representatives of this group, when occurring in the microbial mat community, is the presence of significant amounts of detritus, besides the well preserved frustules. Amongst "lagoonary" diatoms brackish-water ones predominate. They are represented by e.g. *Achnathes brevipes*, *A. lemmermannii*, *Amphora coffeaeformis* (Pl. 4J), *A. holsatica*, *Campylodiscus clypeus*, *C. echeneis*, *Cocconeis scutellum*, *Diploneis didyma*, *D. interrupta* (Pl. 4C), *D. smithii*, *Navicula pygmaea*, *N. humerosa*, *N. peregrina*, and *Nitzschia sigma*. There also single specimens of typical marine forms, e.g. *Actionocyclus ehrenbergii*, *Grammatophora oceanica*, *Diploneis bombus*, *Navicula elegans* occurred. The halophilous ones were represented by *Caloneis amphisbaena*, *Epithemia sorex*, *E. turgida*, *Navicula pusilla*, *N. rynchocephala*, *N. viridula*, *Pinnularia krookii*, and *Rhoicosphenia abbreviata*. The indiffent forms of "lagoonary" diatom group occurred as
numerous species, however, represented by single specimens of e.g. *Achnanthes lanceolata*, *Caloneis bacillum*, *Diatoma elongatum*, *D. vulgare*, *Diploneis ovalis*, *Epithemia intermedia*, *Meridion circulare*, *Navicula cryptocephala*, *N. placentula*, *Nitzschia palea*, *N. sigmoidea*, *N. thermalis*, *Pinnularia interrupta*, *Synedra ulna*, and *Surirella ovata*.

In the Puck Bay mat microbiota scarce planktic forms also occur. These are: *Cyclotella meneghiniana*, *Melosira jürgensii*, *M. moniliformis*, *M. nummuloides*, *Stephanodiscus hantzschii*, and *Thalassiosira decipiens*.

The characteristic feature of the mat diatom community of the Puck Bay is low number of taxa (sometimes less than 20) including 2 to 5 strongly predominating. Their total content in the mat diatom community attains 70—90%. The representatives of the other taxa rarely occur in amounts higher than 5%. The differentiation index \( H' \) of the typical Puck Bay microbial mat community ranges from 2.3 to 2.8. In the diatom community of the central part of Puck Bay bottom deposits a high number of taxa (more than 40) occur. Amongst them forms decidedly dominating are lacking. The percent content of the most abundant taxa did not exceed 20%. Usually content of several species ranged from 10 to 15%. The other taxa were represented by small numbers of specimens. Consequently the differentiation index \( H' \) values of the lagoonary diatom community are much higher and range from 4.2 to 4.5. The increase of the lagoonary forms content in the microbial mat diatom community brought about the rise of \( H' \) values of the latter, up to ca. 3.2. The highest \( H' \) values were mainly observed during the maximum mat development period (August—September).

**MICROBIOTA OF BIOGENIC LAMINATED DEPOSITS**

The community of microorganisms occurring in Holocene laminated deposits is composed of cyanobacteria, green algae, diatoms, euglenophytes and fungi. In the deposits investigated, both coccoid and filamentous cyanobacteria were detected (see Pl. 5). There were recorded the following coccoid cyanobacteria: *Microcystis aeruginosa*, *M. incerta*, *Merismopedia punctata*, *Chroococcus minutus*, *Ch. turgidus*, *Ch. minimus*, *Aphanthece castagnei*, and *Gloeocapsa* sp. Their occurrence was detected amongst both the cultivated samples and those stained with fuchsine-B solution.

The filamentous cyanobacteria of the family Oscillatoriaceae were represented by the genera *Oscillatoria*, *Lyngbya*, *Phormidium*, *Spirulina*. Members of the genus *Oscillatoria* were detected in the culture of one sample. An occurrence of thin-walled sheaths of probable *Oscillatoria* origin was also recorded in fuchsine-B stained preparations. These were of 10 μm in diameter and moreover uneven and folded. These features indicate similarity to sheaths originated as a result of biodegradation in the culture of *Oscillatoria* sp. It can therefore be guessed that the abovementioned sheaths are of the genus *Oscillatoria* affinity. Likewise *Oscillatoria*, representatives of the genus *Lyngbya* occurred in single cultivated sample. In fuchsine-B stained and SEM preparations, however, these
were common. These were thick-walled sheaths of 10 to 15 μm in size, occurring in bunches. Representatives of the genus *Spirulina* were only noted in a few water preparations of suspension prepared (using sterile water) immediately after transfer of the laminated deposits to the laboratory. Unlike the other Oscillatoriaceae, *Spirulina* sp. specimens did not revive in the culture. The single specimen of a shape typical of the genus *Spirulina* was observed in one of SEM preparations. This was a part of trichome including several twists.

Contrary to the aforementioned forms, members of the genus *Phormidium* frequently occurred in the culture. The most common was *Ph. fragile*. Its trichomes of 2 μm in diameter formed characteristic twisting, round structures. Similar forms were also found in SEM preparations. There bunches of trichomes of 2 μm in diameter with characteristic constricted spots were detected. Such forms as *Oscillatoria* sp., *Lyngbya* sp., and *Spirulina* sp. occurred exclusively in the biogenic laminated deposit, whereas *Phormidium* sp. was also recorded in the underlying fine detrital peat.

Representatives of the family Nostocaceae belonged the to genus *Anabaena*. They occurred in cultivated samples of laminated deposits; in terms of cell shape and size they resembled *A. affinis*. Moreover in fuchsine-B stained preparations there frequently occurred single, oval or elliptic-like cells of 10 (16) × 15 (25) μm in size. Their cell wall thickness amounted ca. 2 μm. From above it appears that these might be resting cells of *A. affinis*. The occurrence of *A. affinis* and resting cells is only restricted to laminated deposits.

Amongst microorganisms occurring in biogenic laminated deposits, green algae both coccoid and filamentous were detected (see Pl. 6). In a majority of preparations of cultivated samples and of stained ones there frequently occurred unicellular forms of diameter 12 to 20 μm and smooth cell wall. Comparison of forms present in the culture and those of the modern Puck Bay microbial mat showed their similarity to representatives of the genus *Chlamydomonas*. In the culture these microalgae occurred as single cells or as aggregates of 3 to 6 cells in joint sheath. Moreover, in the culture and in stained preparation, there were observed forms which originated as a result of the fissuring of the aforementioned sheaths. Their size ranged from 20 to 30 μm and their walls were smooth. Only rarely in the culture were these sheaths noted during their abandonment by the mentioned unicellular forms.

In both cultivated samples and stained preparations there were found aggregates of cells all of which possessed characteristic depression several micrometers wide and deep. The cell number changed from 4 to more than 10. The diameter of single cell amounted from 15 to 25 μm, whereas of whole aggregates ca. 50 μm. Similar aggregates were also recorded in SEM preparations. The above presented characteristic shows their similarity to members of the genus *Pandorina*.

Representatives of the Chlorococcales were recorded both in culture and in stained preparations. There were found members of the genera *Botryococcus*, *Coelastrum*, *Pediastrum*, and *Scenedesmus*. In stained preparations *Scenedesmus*
sp. formed aggregates of 3 to 4 cells. With respect to size they can be divided into two groups: smaller ones of \(8 \times 14\) (16) µm resembling those occurring in the cultures \(S. ecornis\), and bigger ones of \(8 \times 21\) (24) µm which indicates similarity to \(S. quadricauda\). Exclusively in stained preparations there were detected numerous aggregates of \(Botryococcus\) sp., and \(Crucigenia\) cf. \(tetrapedia\).

In stained preparations there frequently occurred unicellular forms of likely chlorococcal affinity. Amongst these oval forms of ca. 25 µm in diameter and of thin cell wall occurred. Unicells of similar size and shape are known from the deposits of e.g. Late Precambrian (Knoll & Sweet 1987) and of Jurassic age (Lindgren 1981), and they belong to the genus \(Leiosphaeridium\).

Filamentous green algae of the order Ulotrichales occurred in the cultivated samples. There were detected \(Stichococcus bacillaris\) and \(Ulothrix\) sp. Of these, \(S. bacillaris\) was detected more frequently than \(Ulothrix\) sp., and both of them occurred only in the laminated deposits.

In stained preparations there were found representatives of euglenophytes, belonging to the Trachelomonadaceae. These were sheaths of the genus \(Trachelomonas\). Their length ranged from 30 to 35 µm (Pl. 6); and they were recorded in both laminated deposits and in the underlying peat.

In stained preparations the presence of microfungi and of their resting cells was detected. Unlike cyanobacteria and green algae, fungi in those preparations remained unstained. Their characteristic features were irregularity of hyphae (including branching) and width of 3 to 5 µm. Their resting cells had variable shapes from cup trough spherical to rod (Pl. 6K). The set of fungi of laminated deposits was much less differentiated than in the underlying peat.

In the laminated deposits there were also detected frequently occurring macroalgal remnants (Pl. 6L), which were recorded both in stained and SEM preparations.

Like the diatom community of the modern Puck Bay microbial mat, the one present in Holocene laminated deposits also divides into diatoms typical of the mat environment and of “lagoony” ones (see Tables 1-3 and Pl. 4). A group of diatoms typical of microbial mat is represented in the laminated deposits by \(Achnanthes delicatula\), \(Cocconeis placentula\), \(Fragilaria construens\) v. \(venter\), \(F. virescens\) v. \(subsalina\), \(Navicula cryptolyra\), \(N. protracta\), \(N. salinarum\), \(Opephora olsonii\), \(Synedra pulchella\), and \(S. tabulata\). Amongst these \(O. olsonii\), \(A. delicatula\), \(F. construens\) v. \(venter\) and \(F. virescens\) v. \(subsalina\) predominate. Sporadically in the laminated deposits \(Navicula cryptolyra\) and \(Nitzschia fonticola\) are recorded. In majority of the samples analyzed, \(O. olsonii\) predominated. Its percentages ranged from 2 to 27% (profile A) and from 8 to 36% (profile B). In peat of the profile \(A\), the species \(O. olsonii\) occurs as single specimens, often in a form of detritus. The highest percentage of \(A. delicatula\), up to 15%, was recorded in laminated deposits of the profile \(B\), whereas in profile \(A\) it reached 10%. The most striking feature of the diatom community of the laminated deposits of the profile \(C\) is very low \(A. delicatula\) content. In
Table 1

Percent contents of chosen diatom taxa in the biogenic laminated deposits exposed at Władysławowo (profile A)

<table>
<thead>
<tr>
<th>taxa</th>
<th>depth below surface (cm)</th>
<th>5</th>
<th>7</th>
<th>10</th>
<th>16</th>
<th>20</th>
<th>30</th>
<th>35</th>
<th>40</th>
<th>45</th>
</tr>
</thead>
<tbody>
<tr>
<td>Achnanthes delicatula GHUN.</td>
<td></td>
<td>7</td>
<td>9</td>
<td>10</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Actinocyclus ehrenbergii EHR.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Caloneis bacillum CL.</td>
<td></td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Campylodiscus clypeus EHR.</td>
<td></td>
<td>2</td>
<td>2</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>C. echeneis EHR.</td>
<td></td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cocconeis placenta EHR.</td>
<td></td>
<td>3</td>
<td>2</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>5</td>
<td>+</td>
</tr>
<tr>
<td>C. p. v. euglypta GHUN.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>20</td>
</tr>
<tr>
<td>C. acutellum EHR.</td>
<td></td>
<td>+</td>
<td>2</td>
<td>2</td>
<td>4</td>
<td>12</td>
<td>2</td>
<td>2</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td>Diploneis didyma CL.</td>
<td></td>
<td>+</td>
<td></td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>D. interrupta CL.</td>
<td></td>
<td>12</td>
<td>6</td>
<td>6</td>
<td>44</td>
<td>6</td>
<td>16</td>
<td>19</td>
<td>9</td>
<td>11</td>
</tr>
<tr>
<td>D. smithii CL.</td>
<td></td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Epithemia sorex KUTZ.</td>
<td></td>
<td>+</td>
<td>2</td>
<td></td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td>E. turgida KUTZ.</td>
<td></td>
<td>+</td>
<td></td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fragilaria construens v. venter GHUN.</td>
<td></td>
<td>3</td>
<td>6</td>
<td></td>
<td>5</td>
<td>2</td>
<td>17</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F. virescens v. subsalsa GHUN.</td>
<td></td>
<td>13</td>
<td>4</td>
<td>7</td>
<td>+</td>
<td>2</td>
<td>7</td>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grammatophora oceanica GHUN.</td>
<td></td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>9</td>
<td>3</td>
</tr>
<tr>
<td>Navicula cryptolyra BROCK.</td>
<td></td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>N. elegans W.SM.</td>
<td></td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>N. peregrina KUTZ.</td>
<td></td>
<td>1</td>
<td>4</td>
<td>+</td>
<td>2</td>
<td>+</td>
<td>2</td>
<td>5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>N. pusilla W.SM.</td>
<td></td>
<td>2</td>
<td>3</td>
<td>5</td>
<td>18</td>
<td>2</td>
<td>8</td>
<td>5</td>
<td>5</td>
<td>+</td>
</tr>
<tr>
<td>N. salinarum GHUN.</td>
<td></td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>N. viridula KUTZ.</td>
<td></td>
<td>5</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>10</td>
<td>10</td>
<td>8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nitzschia palea W.SM.</td>
<td></td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>5</td>
<td>28</td>
</tr>
<tr>
<td>Opephora olsenii MOL.</td>
<td></td>
<td>27</td>
<td>19</td>
<td>25</td>
<td>+</td>
<td>24</td>
<td>10</td>
<td>2</td>
<td>17</td>
<td>+</td>
</tr>
<tr>
<td>Pinnularia borealis EHR.</td>
<td></td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2</td>
<td>14</td>
</tr>
<tr>
<td>P. krookii HUST.</td>
<td></td>
<td>7</td>
<td>6</td>
<td>8</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>24</td>
</tr>
<tr>
<td>P. viridis EHR.</td>
<td></td>
<td>3</td>
<td>+</td>
<td>+</td>
<td></td>
<td></td>
<td>20</td>
<td>19</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td>Rhoicosphenia abbreviata LA.-BE.</td>
<td></td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Synedra pulchella RAL.</td>
<td></td>
<td>1</td>
<td>4</td>
<td>5</td>
<td>2</td>
<td>2</td>
<td>+</td>
<td>8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>S. tabulata KUTZ.</td>
<td></td>
<td>2</td>
<td>2</td>
<td>3</td>
<td>+</td>
<td>1</td>
<td>2</td>
<td>5</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 2

Percent contents of chosen diatom taxa in the biogenic laminated deposits (profile B, near Chatupy)

<table>
<thead>
<tr>
<th>taxa</th>
<th>depth below surface /cm</th>
<th>2</th>
<th>7</th>
<th>13</th>
<th>18</th>
<th>20</th>
<th>23</th>
<th>28</th>
</tr>
</thead>
<tbody>
<tr>
<td>Achnanthes brevipes AG.</td>
<td>8.2.4</td>
<td>8</td>
<td>2</td>
<td>4</td>
<td>7</td>
<td>4</td>
<td>3</td>
<td>17</td>
</tr>
<tr>
<td>A. delicatula GRUN.</td>
<td>+ + +</td>
<td>7</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>17</td>
</tr>
<tr>
<td>Amphora robusta GREG.</td>
<td>+ + +</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Campylocentrum clypeus EHR.</td>
<td>+ + +</td>
<td>+</td>
<td>4</td>
<td>3</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>C. echinoides EHR.</td>
<td>+ + +</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Cocconeis placentula EHR.</td>
<td>+ + +</td>
<td>+</td>
<td>7</td>
<td>2</td>
<td>7</td>
<td>8</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>C. acutum EHR.</td>
<td>3 + + +</td>
<td>+</td>
<td>26</td>
<td>21</td>
<td>12</td>
<td>5</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Diploneis didyma CL.</td>
<td>+ + +</td>
<td>+</td>
<td>49</td>
<td>12</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>D. interrupta CL.</td>
<td>+ + +</td>
<td>+</td>
<td>7</td>
<td>2</td>
<td>7</td>
<td>8</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>D. ovalis CL.</td>
<td>+ + +</td>
<td>+</td>
<td>7</td>
<td>2</td>
<td>7</td>
<td>8</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>E. turgida KUTZ.</td>
<td>+ + +</td>
<td>+</td>
<td>7</td>
<td>2</td>
<td>7</td>
<td>8</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Fragilaria brevisetra GRUN.</td>
<td>4 + 3 + 4</td>
<td>+</td>
<td>3</td>
<td>4</td>
<td>5</td>
<td>8</td>
<td>3</td>
<td>+</td>
</tr>
<tr>
<td>P. construens v. venter GRUN.</td>
<td>+ + +</td>
<td>+</td>
<td>10</td>
<td>13</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>P. virescens v. subsulina GRUN.</td>
<td>+ + +</td>
<td>+</td>
<td>2</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Grammatophora oceonica GRUN.</td>
<td>+ 4 + 2</td>
<td>+</td>
<td>15</td>
<td>7</td>
<td>4</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>N. humerosa BREB.</td>
<td>+ + +</td>
<td>+</td>
<td>3</td>
<td>4</td>
<td>6</td>
<td>6</td>
<td>2</td>
<td>+</td>
</tr>
<tr>
<td>N. peregrina KUTZ.</td>
<td>+ + +</td>
<td>+</td>
<td>9</td>
<td>6</td>
<td>6</td>
<td>2</td>
<td>+</td>
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<tr>
<td>N. pusilla W.SM.</td>
<td>+ + +</td>
<td>+</td>
<td>22</td>
<td>3</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>N. viridula KUTZ.</td>
<td>+ + +</td>
<td>+</td>
<td>2</td>
<td>2</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Nitzschia sigmoidea W.SM.</td>
<td>+ + +</td>
<td>+</td>
<td>2</td>
<td>2</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Opephora olsenii MOL.</td>
<td>+ + +</td>
<td>+</td>
<td>27</td>
<td>15</td>
<td>8</td>
<td>37</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Pinnularia borealis EHR.</td>
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<td>+</td>
<td>11</td>
<td>2</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>P. major CL.</td>
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<td>+</td>
<td>11</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>P. viridis EHR.</td>
<td>+ + +</td>
<td>+</td>
<td>33</td>
<td>11</td>
<td>3</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Rhopalodia gibberula O.MUL.</td>
<td>+ + +</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Synedra pulchella RAL.</td>
<td>+ + +</td>
<td>+</td>
<td>3</td>
<td>4</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>S. tabulata KUTZ.</td>
<td>+ + +</td>
<td>+</td>
<td>4</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
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</tbody>
</table>
Table 3

Percent contents of chosen diatom taxa in the biogenic laminated deposits exposed at Chalupy (profile C, Chalupy)

<table>
<thead>
<tr>
<th>taxa</th>
<th>depth below surface /cm</th>
<th>3</th>
<th>6</th>
<th>9</th>
<th>11</th>
<th>13</th>
<th>16</th>
<th>19</th>
<th>33</th>
<th>36</th>
<th>38</th>
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</thead>
<tbody>
<tr>
<td>Achnanthes delicatula GRUN.</td>
<td></td>
<td>+</td>
<td>3</td>
<td></td>
<td>8</td>
<td>8</td>
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<td></td>
</tr>
<tr>
<td>Actinocyclus ehrenbergii EHR.</td>
<td></td>
<td>+</td>
<td>3</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Amphora pediculus GRUN.</td>
<td></td>
<td></td>
<td>+</td>
<td></td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Camphylodiscus clypeus EHR.</td>
<td></td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
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Holocene biogenic laminated deposits

A — Laminated deposits exposed at Władyśławowo (profile A)
B — Outcrop of the laminated deposits of the profile C at Chalupy
C — Close-up of laminated deposits shown in B
Matforming cyanobacteria; scale bar is 10 μm
A — *Chroococcus turgidus*, B — *Oscillatoria tenuis*, C — *Phormidium* sp., D-E — Filamentous cyanobacteria twinning mineral grains, F-G — Filamentous cyanobacteria of the Oscillatoriaceae affinity
Diatoms from the microbial mat and of the laminated deposits; scale bar is 10 µm

A – Compylodicus clypeus; B – Cocconeis scutellum; C – C. pellicula; D – Diploneis interrupta; E – Epithemia turigida; F – E. sorex; G – Cocconeis placenta; H – Nitzchia fonticola; I – Gephyra obscuri; J – Fragilaria viridis v. subalpina; K – Synedra tabulata; L – Achnanthes delicatula; M – Amphora coffeiformis; N – Fragilaria constricta v. centra; O – Nitzschia sp.; P – N. eugamia; Q – Pinnularia viridis
Cyanobacteria from the laminated deposits; scale bar is 10 µm

A — Chroococcus minutus; B: a — Ch. minutus, b — Aphanothece sp.; C — Oscillatoria sp.; D — Lyngbya sp.; E — Sheath of Oscillatoria-like form; F — Phormidium sp.; G-H — Spores of Anabaena cf. affinis; J — Anabaena cf. affinis

A, F, G, H — funisine-B stained preparations; B, C, D, J — preparations from the culture; F — SEM preparation
Green algae, fungi and macroalgal remnants from the laminated deposits; scale bar is 10 μm

A-B — Coccolid forms probable of the genus *Chlamydomonas* affinity; C — *Chlamydomonas* sp. zoosporophores during abandonment of zoosporangium; D — *Scenedesmus* sp.; E — microfossil originated as a result of the fissuring of zoosporangium; F — *Leiosphaeridium* sp.; G — *Ulothrix* sp.; H — *Crucigenia cf. terspedea*; J — *Trachelomonas* sp.; K — spores of microfungi; L — fragment of macroalgal thalli

A, B, C, D, G — preparations from the culture; E, F, H, J, K, L — funksine-β stained preparations
Formation of “spot” structures as a result of unicellular, eukaryotic microalgae degradation; scale bar is 10 μm

A — Predegraded microalgae; B — “spot” structures formed in dry, aerobic conditions (arrow shows the starch granule); C — degradation effect in wet aerobic conditions (arrow points out the translucent rim of the cellular content residuum); D — granular structure of the cell content at the beginning of degradation process; E — “spot” cells from the modern microbial mat sample; F — aggregate of degraded cells indicating the presence of “spot” structures; G — Glenobhotrion acicnignatis Sczepf from Bitter Springs Formation, Australia (courtesy of Professor A. H. Knoll, Harvard University, USA)
FOSSILIZATION PROCESSES

profile B its distribution is rather even, whereas in A and C ones its highest percent contents are detected in the upper part of the profile. The percent content of both Fragilaria species was variable and changed from 2 to 17% of F. construens v. venter and from 2 to 13% of F. virescens v. subsalina. The rest of diatom taxa typical of the microbial mat environment, occurring in the laminated deposits did not attain considerable percent contents. Amongst these only Synedra pulchella reaches 8% (profile A) and 10% (profile C), and S. tabulata 9% (profile C). Besides Cocconeis placentula, Achnanthes delicatula and Opephora olsenii the rest of diatoms typical of the mat environment appear only in the laminated deposits. The above mentioned forms were observed in peat underlying laminated deposits (profile A) as single specimens mostly or as a detritus. However, C. placentula was there very abundant, its percent content amounted 19%.

The group of “lagoonary” diatoms in the laminated deposits was represented by ca. 60 species. The most common and abundant of these were Grammatophora oceanica, Cocconeis scutellum, Diploneis didyma, D. interrupta, Campylodiscus clypeus, Epithemia sorex, E. turgida, Navicula elegans, N. peregrina, N. pusilla, Rhoicosphenia abbreviata. Amongst these D. interrupta is decidedly dominating. Its percent content ranges from 5 to 44% (profile A), 3 to 40% (profile B) and from 1 to 23% (profile C). However, in some samples D. interrupta occurred only as single specimens. The other taxa of these diatom group were present in laminated deposits in much smaller amounts. The most abundant of these were Cocconeis scutellum (2 to 12% in profile A and up to 27% in profile B), Grammatophora oceanica (max. 5%), Epithemia turgida (max. 4%), Navicula elegans (max. 13%), N. peregrina (max. 5%), and N. pusilla (max. 22%). The percent content of the rest of “lagoonary” diatoms rarely reached 1%, these rather occurred as single specimens.

The analysis of percent diatom distribution in the vertical profile indicates characteristic changes. In samples with the predomination of diatoms typical of mat environment, the “lagoonary” ones are less abundant. This relationship is particularly pronounced in the case of Opephora olsenii and Diploneis interrupta percent contents. Generally, the percent content of “lagoonary” forms in the laminated deposits is higher than in modern microbial mat of the Puck Bay coastal shallows. This is also expressed in higher values of differentiation index; the H’ values of the laminated deposits ranged from 3.4 to 4.4 (Text-fig. 4).

The diatom community of the biogenic laminated deposits indicates considerable differences in terms of species composition and differentiation comparing to the underlying peat (profile A). In the peat, only relatively abundant diatoms occur in the upper part of the profile, while in the lower one only sparse specimens were noted and mostly as a detritus. In the upper part of the profile there Nitzschia palea, Pinnularia krookii, P. borealis, P. viridis, and Cocconeis placentula v. euglypta predominated. Besides Campylodiscus clypeus and D. interrupta, the other “lagoonary” taxa infrequently occurred and mostly as a detritus. The most striking feature of the peat profile sole part is the presence of very abundant detritus of C. clypeus (Text-fig. 4).
Fig. 4. Changes of lithology and of the diatom communities as recorded in the profile A at Władysławowo

I. Lithology: 1 — Biogenic laminated deposits, 2 — Silty sand, 3 — Sandy silt, 4 — Fine detrital peat, 5 — Coarse detrital peat

II. Organic matter percent content

III. Differentiation of the diatom community (H') of the laminated deposits: 1 — Average H' value of the spring time microbial mat diatom community, 2 — Average H' value of the microbial mat diatom community during the summer bloom of cyanobacteria, 3 — Average H' value of the Puck Bay inner part bottom deposits diatom community (point D in Text-fig. 1)

IV. Percent content of the most abundant diatom taxa

V. Percent content of diatom taxa in ecological groups: 1 — Marine, 2 — Brackish-water, 3 — Halophilous, 4 — Typical fresh-water
PALEOECOLOGICAL INDICATORS

Amongst cyanobacteria and green algae frequently occurring in laminated deposits euryhaline organisms, which are resistant to salinity changes, predominate decidedly. These can not be considered as adequately accurate paleoecological indicators. However, diatom species composition is closely related to the environmental conditions they are living in. One of the crucial factors influencing diatom distribution is salinity. Owing to this they are commonly used as paleoenvironmental indicators (e.g., Alhonen 1971, Müller 1986).

The euhalobous, i.e. marine diatoms, are represented in the laminated deposits by Actinocyclus ehrenbergii, Diploneis bombus, D. litoralis, Grammatophora oceanica, Navicula elegans, and Amphora robusta. Amongst these only G. oceanica and N. elegans attain considerable percent contents. In the vertical profile marine diatoms appear barely in laminated deposits. These belong exclusively to the group of “lagoonary” forms (Text-fig. 4).

The mesohalobous (brackish-water) diatoms represent both the group of diatoms typical of mat environment and the “lagoonary” one. The percent content of brackish-water taxa in the laminated deposits range from 34 to 48% (Text-fig. 4). A majority of these typical of the Puck Bay microbial mat, occurring in the laminated deposits, i.e. Achnanthes delicatula, Navicula cryptolyra, N. salinarum, Nitzschia fonticola, Opephora olseni, Synedra pulchella and S. tabulata, are according to their salinity requirements, mesohalobous forms. The mesohalobus forms also constitute the most abundant part of the “lagoonary” diatom group of the investigated deposits. These are represented by e.g. Achnanthes brevipes, A. lemmermannii, Cocconeis scutellum, Diploneis didyma, D. interrupta, D. smithii, Mastogloia braunii, M. pumila, Navicula humerosa, N. peregrina, Campylosticus clypeus, and C. echeneis.

The halophilous (fresh-water, thriving in brackish-water) forms were represented in laminated deposits by several taxa of “lagoonary” group i.e. Cocconeis pediculus, Epithemia sorex, E. turgida, Navicula pusilla, N. rynchocephala, N. viridula, Pinnularia krokii, and Rhoicospenia abbreviata. The most abundant of these were N. pusilla, N. rynchocephala and P. krokii. Excluding P. krokii, their highest percent contents were detected in laminated deposits. The highest content of P. krokii was noted in fine detrital peat. The share of halophilous taxa in the community of the laminated deposits ranged from 12 to 22% (Text-fig. 4). They were nearly exclusively represented by “lagoonary” forms. Amongst halophilous taxa of typical mat diatoms occurring in the laminated deposits only Fragilaria virescens v. subsalina attained appreciable amounts (max. 15%, Table 2). The other of these, i.e. Navicula protracta, was detected only in one sample.

Indifferent (typical fresh-water) diatoms of the laminated deposits are represented by members of both “lagoonary” and typical of mat environment groups. To the latter group belong Cocconeis placentula and Fragilariella
construens v. venter. The group of “lagoonary” forms is represented by e.g. *Caloneis bacillum*, *Diploneis ovalis*, *Epithemia intermedia*, *Fragilaria construens* v. *binodis*, *F. brevistriata*, *Navicula cryptocephala*, *N. placentula*, *N. scutelloides*, *Nitzschia palea*, *N. sigmoidea*, *Pinnularia borealis*, *P. major*, *P. viridis*, *Rhopalodia gibba*, and *Synedra ulna*. These are represented by numerous taxa, which constitute from 29 to 47% of the total number of taxa occurring in laminated deposits, however, they are mainly recorded as single specimens. The percent of only a few of them exceeded 5% (e.g. *P. borealis* in profiles *B* and *C*, and *P. viridis* in profiles *A* and *B*; see Tables 1—3).

The characteristic feature of the laminated deposits diatoms is (with an exception of the lowermost part of the profile *C*) the negligible content of planktic forms. These are represented by single specimens of *Actinocyclus ehrenberghii*, *Thalassiosira* sp., *Melosira granulata* and small amounts of unidentified detritus of centric diatoms, whereas in the lowest part of the profile *C* planktic diatoms frequently occur (e.g. *Coscindiscus commutatus*, *Melosira* spp., *Thalassiosira baltica*) and numerous detritus of the Centricae. Moreover this part of the profile *C* differs with respect to the ratio between “lagoonary” diatoms and those typical of the mat environment. The diatom community of these deposits is composed of much higher number of taxa, with those of “lagoonary” group predominating. Amongst the latter, *Diploneis interrupta* is strongly prevailing. On the other hand, in the upper part of the profiles *B* and *C* a higher percent content of aerophilus diatoms (i.e. *Hantzschia amphioxys* and *Pinnularia borealis*) was noted. Their share in the laminated deposits amount 4 and 22% of *H. amphioxys* and *P. borealis*, respectively. The content of these in the profile *A* is less pronounced (Tables 1—3).

**PROCESSES OF DEGRADATION**

In cultivated samples of the laminated deposits there occurred numerous cyanobacteria and green algae, the most of these was subject to degradational processes. However, the most interesting results were reached in experiments performed with unicellular green algae (see Pl. 7). In the course of microscopic observation there was detected in the investigated samples the presence of “spot” structures. These microalgae both in culture and in samples of the Puck Bay microbial mat occurred as single cells or (more frequently) as aggregates of variable cell number. The diameter of single cell ranged from 10 to 16 μm. On the basis of comparisons with specimens observed in the modern mat material they were tentatively identified as resting cells of representatives of the genus *Chlamydomonas*.

At the initial phase of degradation, internal bodies possessed a distinct granular texture. Following the decrease of their size, this feature tended to disappear gradually. Finally the degraded cell content formed a narrow, homogenous rim round the placed inside “spot” structure. The iodine tincture staining revealed that “spot” structures are granules of starch. This means that
these are remnants of storage substance of eukaryotic microalgae, which is connected with pyrenoide.

Cells containing internal “spot” structures were also found in samples of the modern microbial mat of the Puck Bay. They were observed e.g. in sample of May 1987 taken from the surface of the mat situated above the water level. With respect to size and shape they closely recall those of the cultivated samples of the laminated deposits.

The “spot” structures obtained in the course of degradation experiments in aerobic conditions indicate their close resemblance to those occurring in the fossil state. Microfossils of this type frequently occur in formations of the Proterozoic stromatolites, e.g. in Bitter Springs, Australia (SCHOPF 1986, Oehler 1977, KNOLL 1983), the South Urals (SERGEEV & KRYLOV 1986), Gunflint Formation (KNOLL & al. 1978), and in coeval deposits of Belcher Island, Canada (HOFFMANN 1976). The resemblance of the experimental “spot” structures to those occurring in the fossil state is particularly pronounced in the case of Glenobotrydion aenigmatis SCHOPF and G. majorinum SCHOPF & Blacic.

It seems that of decisive influence on this type of preservation might have been the gradual shrinkage of the cell content under oxygen limited conditions. In the natural environment, the formation of “spot” structures could be the result of oxygen-mediated decomposition in the microbial mat temporarily placed above the water level.

DISCUSSION

The comparison of the results of the reported studies carried out in the Puck Bay area with those from the literature, concerning the microbial mats of other areas, indicates that the mat developing in the study area possesses all features which are considered typical of this type of sedimentary environments. This concerns mats of both carbonate deposits (e.g. GOLUBIC 1973, 1976; COHEN & al. 1977; GERDES & al. 1985) and clastic ones (GUNATILAKA 1975, SCHWARZ & al. 1975, JAVOR & CASTENHOLZ 1981, GERDES & al. 1984b, CAMERON & al. 1985). The main factor limiting the extent of direct comparisons of the structure and origin of the studied mat and those referred to is climate. The majority of the quoted references concern those occurring in an arid climate where the process of the microbial mat development is continuous. Contrary to this in a moderate climate, such as that of Puck Bay, the microbial mat is subjected to changes along with the vegetation season. GERDES & al. (1984b) determine this phenomenon as “low rate and episodic sedimentation”. Moreover the compared mats differ on account of proportion of quantitative contents of main matforming microorganism groups. In hypersaline environments, cyanobacteria prevail the whole year round, whereas diatoms are less abundant and green algae occur sporadically. In the communities of hypersaline environments microbial mats, filamentous cyanobacteria of the genera Microcoleus, Lyngbya, Oscillatoria, Phormidium, and Schizothrix predominate (e.g.,
GOLUBIC 1976, KRUMBEIN & al. 1977, STOLZ & MARGULIS 1984, EHRLICH & DOR 1985). In the studied area, however, they predominate only during the summer bloom of cyanobacteria (i.e. late August — early September). As regards species composition, the community of the Puck Bay matforming microorganisms, demonstrates the closest resemblance to communities occurring in versicolored sands (Farbstreifen Sandwatt) of the German North Sea tidal flats (HOFMANN 1942, KONIG 1982).

The studies of the modern Puck Bay microbial mat make possible the reconstruction of environmental conditions under which the Holocene laminated deposits were formed. The characteristic feature of the studied mat in its spring period of development is low organic matter content (below 1%), which is of autochthonous origin. In the species composition diatoms and green algae predominate, while cyanobacteria are mainly represented by coccoid forms. Amongst diatoms, most typical forms decidedly prevail. The domination of *Achnanthes delicatula* over *Opephora olsenii* is also recorded. The strong predominance of several diatom taxa and small number of species (sometimes less than 20) has the effect that the diatom community differentiation index (H') reaches its lowest values (2.3 to 2.8). Quantitatively, diatoms typical of the microbial mat environment constitute up to 90% of the community. An insignificant share of filamentous cyanobacteria and organic matter content cause that at spring time microbial mat can be destroyed by waves and macroand meiofauna occurring in masses. The mat fossilization potential at that time is negligible. Further development of the mat causes the increase of filamentous cyanobacteria and of organic matter content up to 10%.

The studied mat attains its maximum development during the summer bloom of cyanobacteria. At that time at the bottom surface of the Puck Bay coastal shallows there a cover of ca. 2.0 cm thick is formed. Besides live microorganisms this is composed of abundant degradation products, extracellular excretions, macroalgal and higher plant detritus. A rise in the organic matter content of up to 50% is noted. As a result of the high rate of biodegradation large quantities of hydrogen sulfide are emitted and eutrophic conditions come about. Such a drastic variation of the trophic status of the environment brings about changes within the matforming community. There a decrease of green algae and to a lesser extent of diatoms is noted. On the other hand, the content of filamentous cyanobacteria increases significantly and the presence of euglenophytes is noted (sometimes in masses). Amongst filamentous cyanobacteria representatives of the genera *Lyngbya, Oscillatoria, Phormidium* predominate. At that time also, the mat diatom community is subject to radical changes. The hitherto dominating *Achnanthes delicatula* is being replaced by *Opephora olsenii*. Moreover, the number of "lagoonal" taxa increases. Their increase raises the value of the differentiation index up to more than 3.2. Nonetheless species typical of the microbial mat environment still constitute up to 70% of the diatom community. Hydrogen sulfide emitted in processes of biodegradation makes possible the mass occurrence of purple
sulfur bacteria and chemoautotrophic bacteria of the genus *Beggiatoa*. A high concentration of toxic compounds nearly completely eliminates macro- and meiofauna, which usually dwell and feed in masses within the microbial mat, from the mat ecosystem. GERDES & *et al.* (1984b) designate this type of a mat as the "killer mat".

In spite of the fact that the Puck Bay is a non-tidal basin, its water level is subject to fluctuations. Their amplitude changes from several to ca. 50 centimetres. The water currents generated during water level changes of high amplitude are mainly responsible for the mat burial. This process starts along with the mat exposure caused by the bay water level decrease. Significant admixture of quartz grains with unpolished surface indicates that at beginning, aeolian transport plays a certain role in the process of the mat burial. Admixtures of aerophilous diatoms (i.e. *Hantzschia amphioxys* and *Pinnularia borealis*) within the laminated-deposits diatom community indicate that before being buried microbial mats were emerged. The fundamental stage of the mat covering begins with the repeated rise of the water level in the bay. The sediment particles transported by currents cover the microbial mat. These are transported as mesoripplesmarks of several tenths of meters in length and more than ten centimeters high. A considerable number of "lagoonly" forms amongst the diatom community of the biogenic laminated deposits indicates that mat burying sediment was replaced from the southward situated central part of the bay. The suggestion of mechanical transport is supported by the high content of crushed frustrules of "lagoonly" diatoms of the laminated deposits.

The species composition of microbiota of the laminated deposits indicates that their organic matter content was deposited as a result of the microbial mat burial during summer cyanobacterial bloom. This is supported by the predominance of *Opephora olsenii* amongst diatoms, frequently occurring filamentous cyanobacteria and the high content of amorphous organic matter.

The position of the laminated deposits above the present Puck Bay water level suggests that these deposits originated at generally higher level of waters in this area.

**CONCLUDING REMARKS**

The sedimentological and geomicrobiological studies of the microbial mat developing in the Puck Bay clastic sediments and of Holocene siliciclastic, laminated deposits, indicate the genetic relationship of laminated deposits with fossil microbial mat. It was discovered that, in spite of widespread negative opinions, the preservation potential of microbial mat of clastic sediments is relatively high.

The Puck Bay microbial mat differs from its arid climate counterparts with respect to ratios between main groups of matforming microorganisms. Different is also the mechanism of laminated structure formation, which in the moderate climate of the Puck Bay area is episodic.
The studied mat is subject to cyclic changes. In spring, mat is composed of cyanobacteria (mostly coccoid), green algae and diatoms. The diatom community with very low number of taxa is dominated by *Achnanthes delicatula*. The period of maximum mat development falls in summer bloom of cyanobacteria. At that time the mat biota are dominated by filamentous cyanobacteria of the genera *Lyngbya, Oscillatoria,* and *Phormidium*. Amongst diatoms prevailing to date, *A. delicatula* is being replaced by *Opephora olsenii*.

During the summer cyanobacterial bloom the studied mat possesses highest preservation potential. This is favored by:

- significant organic matter content (particularly amorphus degradation products),
- coherence of the mat structure,
- creation anoxygenic conditions as a result of organic matter decomposition,
- elimination of macro- and meiozoobenthos by toxic compounds from the mat environment,
- microbial mat burial by the sediment and its isolation from the influence of external factors.

In the Holocene laminated deposits, numerous cyanobacteria, green algae and diatoms typical of modern microbial mat environment were recorded. Amongst these only diatoms are of paleoenvironmental significance. Of particular meaning is *Opephora olsenii*, which is the most characteristic from of the maximum stage of mat development. It is therefore proposed *O. olsenii* biofacies as being indicative of the Baltic Sea microbial mats developing in clastic sediments. As Sunbäck (1987) has recently shown, *O. olsenii* is a very common epipsammic diatom in the Baltic Sea littoral, but because of small size it was in the diatom analyses overlooked or misinterpreted.

The experiments performed under laboratory conditions allowed to discover convincing arguments that Proterozoic "spot" cells might have originated as a result of the decomposition of eukaryotic microorganisms related to green algae. It was detected that “spot” structures were formed as a result of cellular content shrinkage in aerobic conditions. The “spot” structures are composed of starch, which is a pyrenoide related storage substance of eukaryotic algae.

In conclusion, it must be stressed that versatile analysis of laminated deposits allowed to discover that the latter originated as a result of burial of the microbial mats developing in clastic sediments of moderate climate. The presented results encourage the possibility to undertake more detailed studies of fossil, organic matter laminated sandstones (siliciclastic stromatolites).

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26 ANDRZEJ WITKOWSKI


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A. WITKOWSKI

PROCESY FOSYLIZACJI MATY MIKROBIOTYCZNEJ
W OSADACH KLASTYCZNYCH ZATOKI PUCKIEJ

(Streszczenie)

Przedmiotem badań są procesy rozwoju i degradacji współczesnej maty mikrobiotycznej z osadów klastycznych przybrzeżnych płyniących Zatoki Puckiej, a także holocenskie laminowane osady biogeniczne (patrz fig. 1—4, tab. 1—3 oraz pl. 1—7). W wyniku przeprowadzonych badań sedymnetologicznych oraz geomikrobioiiologicznych stwierdzono, że osady laminowane powstały w rezultacie fosylizacji mat mikrobiotycznych. Wskazują na to cechy teksturalne osadów (laminacja, wysoka zawartość materii organicznej) oraz skład gatunkowy występujący w tych osadach mikroskamieniałości, wśród których najliczniej występują sinice, zielonki i okrzemki. Sinice nitkowate reprezentowane są przez formy należące do rodzajów *Lyngbya*, *Oscillatoria*, *Phormidium* i *Spirulina*. W okresie letniego zakwitu sinic (przelom sierpnia i września) są one mikroorganizmami dominującymi w składzie maty mikrobiotycznej. Przewaga *Opephora olsenii* wśród okrzemek oraz względnie duży udział sinic nitkowatych wykazują, że osady te tworzyły się w rezultacie fosylizacji mat mikrobiotycznych w stadium ich maksymalnego rozwoju, tj. podczas zakwitu sinic. W tym czasie badana mata posiada najwyższy potencjał fosylizacyjny. Procesowi fosylizacji sprzyja: wysoka zawartość materii organicznej, eliminacja zoobentosu z zespołu maty, niska aktywność czynników hydrodynamicznych oraz szybkie przysypanie maty przez osad. Powstanie holocenskich osadów laminowanych jest związane ze wzrostem poziomu wód Zatoki Puckiej, który miał miejsce w ostatnim tysięcleciu.