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The dasycladacean nature of Late Paleozoic palaeoberesellid algae

ABSTRACT: The exceptionally well preserved moulds of problematic microfossils from the tribe Palaeoberesellae MAMET & ROUX 1974, were found in the Lower Carboniferous limestones in the Lublin Coal Basin and in the Sudetes in Poland. The morphology of moulds allowed to state a dasycladacean affinity of the group, which previously was assigned not only to the calcareous algae, but also to the foraminifers and even to the sponges. The recognition of the dasycladacean nature of the tribe Palaeobereselleae evidences precisely their role as a paleoenvironmental indicator, what is exemplified by the Waulsortian buildups in Western Europe.

INTRODUCTION

The tubular benthic microorganisms, preserved in the form of calcareous perforated tubes, and internally segmented by transverse annular partitions, have composed one of the most frequent biotic components in the shallow water areas of the Devonian and Mississippian seas. In the formal sense of taxonomy this group of microfossils is classified as the tribe Palaeobereselleae MAMET & ROUX 1974. Informally, it has been named the palaeoberesellid or the kamaenid group. All the hitherto made observations were based on investigations of thin sections, and they allowed to note a great internal differentiation in this group, what was supported by the abundance of species and genera, viz. Anthracoporellopsis MASLOV 1956, Kamaena ANTROPOV 1967, Exvotarisella ELLIOTT 1970, Pseudokamaena MAMET 1972, Kamaenella MAMET & ROUX 1974, Palaeoberesella MAMET & ROUX 1974, Parakamaena MAMET & ROUX 1974, Subkamaena BERCHENKO 1981, Brazhnikovia BERCHENKO 1981. Stylaella BERCHENKO 1981. Triangulinella MAMET & PREAT 1985, and (connected with them) Cribrokamaena BRENCKLE 1985 and Crassikamaena BRENCKLE 1985. Despite of larger and larger amount of papers concerning taxonomical affiliation of the palaeoberesellids, this problem is still unsolved both in general, either animal

or plant attribution, and in a more detailed sense of their taxonomical position.

The material presented in this paper and coming from the Lower Carboniferous deposits of Poland, affords new, probably decisive arguments which indicate an algal nature of the palaeoberesellids. The hereafter described specimens were prepared primarily from the Carboniferous Limestone beds of the Lublin Coal Basin (SE Poland) and, partly, from those exposed at Srebrna Góra (Bardo Mts, Sudetes). The Carboniferous Limestone beds of the Lublin Coal Basin are lithostratigraphically included into the parallic, Limestone-Claystone Series (see PORZYCKI 1980), which is characterized by the Yoredale type of cyclic sedimentation, and which chronostratigraphically corresponds to the uppermost Viséan.

An extraordinary state of preservation of the algae in these deposits allowed the author (SKOMPSKI 1981, 1984) to revise a few genera, among others *Calcifolium* and *Kulikia*. The sedimentary environment of the Lower Carboniferous algal limestones and paleontological characteristics of their algal content were also presented by the author in other earlier papers (SKOMPSKI 1985, 1986).

PREVIOUS OPINIONS ON THE NATURE OF PALAEOBERESELLIDS

The specimens included recently in the tribe Palaeobereselleae were primarily recognized as foraminifers by EHRENBERG (1854) and von MÖLLER (1879). The foraminiferal affiliation of these microfossils, based on a general morphological affinity, persisted a long time, and in many descriptions these forms have usually been assigned to the genera Nodosinella and Moravammina (e.g. FOMINA 1960, AIZENVERG & BRAZHNIKOVA 1966, MENNER & REITLINGER 1971, TOMAS 1974). Their algal nature was suggested by MASLOV (1956) and ANTROPOV (1967), who created the new genera Anthracoporellopsis MASLOV, and Kamaena ANTRO-POV. An essential argument indicating their algal affinity was the presence of pores oriented perpendicularly to the calcareous wall of the tube. The genus Anthracoporellopsis was characterized by dichotomously branching pores, whereas the pores in Kamaena were straight (unfortunately these descriptions were not confirmed in illustrations). RIDING & JASNA (1974) classified the genus Uraloporella KORDE, 1950, together with Anthracoporellopsis and Kamaena. The well--marked septa of Uraloporella and a questionable porosity of the wall, determined these authors to negate an algal affinity of the whole group (cf. also RIDING 1977); the classification of palaeoberesellids was left an open question, but some similarities to the foraminifers (microstructure of the wall) were pointed.

MAMET & ROUX (1974) made a general revision of the discussed group of microfossils, and they created three new genera, Kamaenella, Palaeoberesella and Parakamaena, included into the new tribe Palaeobereselleae together with Kamaena, Anthracoporellopsis, Exvotarisella and Pseudokamaena. This group, assigned with a doubt to the order Dasycladales, was recognized as ancestors of the dasycladacean group Bereselleae, which expanded in the Upper Carboniferous. However, MAMET & ROUX (1974) did not dispel doubts relating porosity of the wall, because only some twenty of several hundred of excellent micrographs showed irregular and fragmentary pores.

The third concept of classification of the palaeoberesellids appeared when TERMIER, TERMIER & VACHARD (1975; see also 1977) included all the above indicated genera to the new family Moravamminidae, which was classified within the group of the sponges Ischyrospongia. The Moravamminidae differ from the foraminifers (according to TERMIER, TERMIER & VACHARD 1977) by: "lack of proloculus, by the branching mode of perforations and frequent forking"; transverse septation and the microstructure of the wall were the main features differing them from the fossil algae.

The investigations in the 80's allowed to distinguish several hitherto unknown genera within the tribe Palaeobereselleae, but any new ideas of classification did not appear. VACHARD (1980) was still including the palaeoberesellids to Algospongia, and he even expanded this thesis by an illustration of a hypothetical phylogenetic relationship between the families Moravamminidae and Aoujgaliidae. LEES, HALLETT & HIBO (1985) supported this idea on the basis of a growth model of the Waulsortian buildups. They argued that the both families are found together, below the photic zone, and distribution of the moravamminids is reminescent of the pattern shown by sponge spicules. ZADOROZHYJ & YUFEREV (1980) and BERCHENKO (1981) stated precisely the rules of distinguishing the particular species and genera within the tribe Palaeobereselleae, and they consistently numbered this tribe to the order Dasycladales. Contrary to them, BASSOULLET & al. (1979) exluded this group from the fossil dasycladacean algae. Nevertheless, MAMET & ROUX (1981) strongly advocated a position of the palaeoberesellids within the green algae (cf. also ROUX 1985, MAMET & PREAT 1985). and added some new arguments for such an attribution, viz. the presence of presumable conceptacles in the wall in the genus Palaeoberesella (MAMET & ROUX 1981, Pl. 1, Fig. 2).

The present state of discussion is the best characterized by BRENCKLE (1985, p. 56), who stated that "...the palaeoberesellids and their descendants, the Bereselleae, should be united in a new family or higher taxonomic group, but left questionably within the Chlorophyta until phyletic relationships are established...".

Some specimens of palaeoberesellids from the Lublin Coal Basin (mainly those in thin sections) were previously reported by the author (SKOMPSKI 1986). The most important hint for considerations on the nature of these fossils was a finding of a reticular structure of the palaeoberesellid wall. This feature is clearly visible in reflected light and it explains an effect of the wall porosity seen in transverse sections. In conclusion, an affinity of the Palaeobereselleae was stated (SKOMPSKI 1986, p. 265) "to the red algae of the family Ungdarellaceae...", although this opinion was regarded as "highly speculative in the present knowledge of calcareous algae...".

PALAEOBERESELLIDS FROM THE LUBLIN COAL BASIN AND SUDETES

MATERIAL

The investigated specimens (see Pls 1—6) have been prepared mainly from the Upper Viséan organodetrital limestones pierced by the boreholes Orzechów IG-2, Sawin IG-3 and Sawin IG-7 in the northeastern part of the Lublin Coal Basin. In these limestones it is possible to distinguish five microfacies; the algal MF, the foraminiferal MF, the crinoid MF,

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the spiculitic MF, and the most frequently the organodetrital MF, which is composed of mixed elements of other microfacies. The algal MF is characterized by the occurrence of more than 20 taxa (SKOMPSKI 1986), among which dominate the phylloid algae *Calcifolium*, and rarely present are the palaeoberesellid algae, especially those of the genus *Kamaena*.

The investigated material contains both the specimens recognized in thin sections as well as those chemically prepared with aim of 10% acetic acid. Due to a varying stage of neomorphism, some specimens in thin sections display a clear, sparitic wall, while the others are microsparitic or partly sparitized (see Pl. 1 and Pl. 2). A reconstruction of the primary, real shape of the "cells" (determined by wall and partitions) is frequently possible in reflected light (Pl. 1, Figs 1b, 2b, 4b; Pl. 2, Figs 2b, 5b; see also SKOMPSKI 1986, Pl. 5, Figs 5-6; Pl 6, Figs 3-4). The sections tangential to the surface of tubes enable to show a reticular structure of the wall (Pl. 1, Figs 1-3). The interior of tubes is usually filled with the same material as that surrounding the specimens, but sometimes it is entirely sparitized (Pl. 2, Fig. 3) or pyritized (arrowed in Pl. 2, Fig. 2a). The latter specimens are extremely useful for morphological reconstructions of the living parts of the plant, because during dissolution of limestones a fine-grained wall of the tube has been corroded earlier than coarse-grained sparitic internal moulds (e.g. those presented in Pls 3-6). One specimen (illustrated in Pl. 3, Figs 1a-1b) is particularly valuable, because it was originally composed of two parts (moulds and calcareous reticulate wall), which have been separated during preparation of the specimens for SEM. In general, more than 100 moulds were the subject of investigations in SEM, but all of these specimens have been prepared from samples which in the thin sections consisted only of single, isolated palaeoberesellids (3-5 specimens in standard thin section). Apart from palaeoberesellids (mainly Kamaena), the only distinguishable forms were the foraminifers (e.g. Archaediscus, Howchinia, Eostafella, Endothyra, Tetrataxis), phylloid algae (Calcifolium okense), and fragments of crinoids.

Some moulds (Pl. 3, Fig. 2 and Pl. 4, Figs 1, 5) have been prepared from the Lower Carboniferous limestones exposed at Srebrna Góra in the Bardo Mts (Sudetes). These rocks are characterized by a higher degree of neomorphism and they represent the biomicrosparitic MF with fragments of crinoids, tabulates, brachiopods, sponge spicules and single unicellular foraminifers. The walls of rare palaeoberesellids are herein yellowish and sparitic.

MORPHOLOGY OF MOULDS

At first glance, the dasycladacean type of morphology is clearly visible on the investigated moulds: verticils of ramifications branch out of the central stem, and therefore the dasycladacean terminology is used in the following description.

In general, all the 1st order ramifications are distributed in the form of verticils, among which it is possible to distinguish three types (Text--fig. 1): the single-row verticils, the double-row verticils, the composite verticils.

In the single-row verticils, ramifications are distributed in the plane perpendicular to the axis and in the equal distance one from another (Pl. 6, Figs 1--2,



Palaeoberesellid algae, Kamaena delicata ANTROPOV 1967, in thin sections, in transmitted (a) and reflected (b) light

1-3 — Longitudinal, slightly oblique sections through curved parts of tubes (reticular structure of wall is visible), 1 — specimen from borehole Sawin-7 (depth 1083 m), \times 30; 2 — enlarged part of Fig. 1, \times 60; 3 — specimen from Podedwórze-2 (depth 584 m), \times 40

4 — Longitudinal sections, specimens from borehole Sawin-3 (depth 1137 m), imes 30

Different stages of preservation of palaeoberesellid algae in thin sections, in transmitted (a) and reflected (b) light

1, 4-5 — Sections with partly sparitized internal parts of tube, thin neomorphic layer is visible on some partitions (Figs 1 and 4); 2 — Section with partly pyritized (arrowed) internal part; 3 — Section with totally sparitized internal part; 1-4 — specimens from borehole Sawin-3 (depth 1137 m), 1 taken $\times 60$, 2-4 taken $\times 30$; 5 — from Sawin-7 (depth 1069 m), $\times 60$

1 — Mould of palaeoberesellid alga, characterized by composite type of verticils (Fig. 1a) and fragment of calcareous sleeve with reticular structure (Fig. 1b); specimen from borehole Orzechów-2 (depth 918 m), × 125

2-4 — Moulds with double-row verticils of branches (Fig. 3b — reconstruction of calcareous sleeve on the mould figured in 3a); 2 — specimen from Srebrna Góra, ×150; 3 — from borehole Orzechów-2 (depth 918 m), ×100; 4 — from Sawin-7 (depth 1069 m), ×100

1-3 - Moulds of palaeoberesellid algae, characterized by composite verticils (Fig. 1b — reconstruction of calcareous sleeve on the mould figured in 1a; Fig. 1c —

 4-5 — Moulds with double-row verticils of branches (Fig. 5b — reconstruction of calcareous sleeve); 4 — specimen from Orzechów-2 (depth 918 m), × 70; 5 specimen from Srebrna Góra, imes 135

Different types of verticils of palaeoberesellid algae: 1-3, 7 — double-row verticils, 4-5 — composite verticils, 6 — double-row or composite verticils 1 — Enlarged part of specimen presented in Pl. 4, Fig. 4, × 140; 2 — enlarged part of specimen

1 — En!arged part of specimen presented in Pl. 4, Fig. 4, × 140; 2 — enlarged part of specimen presented in Pl. 3, Fig. 2, × 300; 3 — specimen from borehole Sawin-3 (depth 1137 m), × 200;
 4 — from Orzechów-2 (depth 913 m), × 150; 5 — enlarged part of specimen presented in Pl. 3, Fig. 1a, × 170; 6 → specimen from Orzechów-2 (depth 913 m), × 180; 7 — enlarged part of specimen presented in Pl. 3, Fig. 3a, × 130

1-2, 6 — Moulds with single-row verticils of branches: 1-2 — specimens from borehole Orzechów-2 (depth 918 m), × 100; 6 — from Sawin-7 (depth 1069 m), × 90
3, 5, 7 — Moulds with composite verticils, specimens from Orzechów-2 (Fig. 3 from depth 918 m, × 150; Figs 5 and 7 from depth 913 m, × 75)
4 — Mould with double-row verticils, from Orzechów-2 (depth 910 m), × 125

6). The interverticil distance corresponds usually to the diameter of the central stem (Pl. 6, Figs 1-2), but sometimes it is considerably smaller (Pl. 6, Fig. 6).

In the double-row verticils (Pl. 3, Figs 2-4; Pl. 4, Figs 4, 5[?]; Pl. 5, Figs 1?, 2-3, 6?, 7; Pl. 6, Fig. 4), ramifications are arranged in two symmetrical and adjoining whorls, in which particular branches are generally coupled (Pl. 5, Figs 2-3 and 7). Sometimes, this symmetry is not precise what could be caused by a poor state of preservation. The interverticil distance is usually similar to the width of verticils and it is significantly smaller (1/3 or 1/4) than the diameter of the central stem.

In the composite verticils there are at least two types of distribution: either ramifications are arranged irregularly (Pl. 3, Fig. 1a; Pl. 4, Fig. 1; Pl. 5, Fig. 5), or they are situated in a few adjoining whorls. Particular, corresponding ramifications from different whorls are often jointed and they form small rolls, parallel to the main axis of the alga (Pl. 4, Figs. 2—3; Pl. 5, Fig. 4; Pl. 6, Figs! 3, 5 and 7). The interverticil distance is always distinctly smaller than the width of verticils.

Fig. 1. Types of verticils and calcareous sleeves

A — single-row verticils, B — double-row verticils, C_1 — composite verticils with branches distributed in the form of rolls, C_2 — composite verticils with irregularly arranged branches; A', B', C' — hypothetical reconstructions of calcareous sleeves, corresponding with particular types of verticils

The shape of 1st order ramifications is pretty much the same in each type of verticils; straight, elongated, and cylindrical. Their length is difficult to estimate due to corrosional character of specimens; only in a few cases (Pl. 3, Fig. 1 and Pl. 5, Fig. 5) some ramifications have preserved their primary length.

The measurements of specimens change on a large scale and they are not dependent on the type of verticils. A diameter of the central stem ranges from 40 to 230 μ m, whereas the external diameter of the verticil changes from 80 to 350 μ m.

A CONSTRUCTION IN THE PALAEOBERESELLIDS

A comparison of informations yielded both by thin sections and by prepared specimens allows a reconstruction of the main features of the palaeoberesellid structure (Text-fig. 2). These algae were characterized by a construction typical of the euspondyl Dasycladaceae, but calcification did not occur around each ramification. This process usually took place outside of the central stem and on the surface of the whole verticil. The only exception seems to be the genus *Exvotarisella*, in which calci-

Fig. 2. Scheme of construction of the palaeoberesellids \mathbf{s} — calcareous sleeve, $\mathbf{R1}$ — 1st order ramification, $\mathbf{R2}$ — 2nd order ramification fication penetrated the interior of verticil and it surrounded the particular branches. In the interverticil segments the calcareous sleeve was distinctly thicker than in parts corresponding to the verticils, but the external diameter of tubes was constant, what in consequence gave an effect of internal partitions. The calcareous sleeve was composed of wide reticular (pseudoporous) sections, homologous with verticils, and narrow, smooth sections without "pores", homologous with interverticil areas. The second-order ramifications, hypothetically reconstructed in a trichophorous form (Text-fig. 2), probably projected though reticular parts of the sleeve.

PROBLEMS OF TAXONOMY

The taxonomy of any group, based only on the features recognizable in thin sections, will always cause doubts, because the differentiation of sections is usually greater than the variety of real forms in a particular fossil. Difficulties in finding a relation between thin sections and spatial forms of Paleozoic foraminifers could serve as an especially good exemplification of this problem. On account of a generally smaller number of investigations these difficulties concern also calcareous algae, what could be supported, for example, by the discovery of real morphology of the genera *Calcifolium* and *Kulikia* in the Viséan deposits of the Lublin Coal Basin. In the case of the tribe Palaeobereselleae, a relation between thin sections and prepared specimens is also unidirectional, *i.e.* it is possible to find the shape of sections of the calcareous sleeve on basis of internal moulds (see Pl. 3, Fig. 3 and Pl. 4, Figs 1, 5), but inversely it is difficult.

According to MAMET & ROUX (1974), the taxonomy of the tribe Palaeobereselleae was based mainly on the shape of "cells" and transverse partitions, type of porosity and on the measurements of specimens. In the light of the above presented data on the dasycladacean nature of discussed forms, all of these features are questionable (cf. SKOMPSKI 1986). Particular parameters of tubes and "cells" are dependent on the plane of section, and thus they are rather accidental. The type of verticils, which should be regarded as a principal feature of the palaeoberesellids, is also independent of the measurements and it does not correspond with the shape of "cell" and tube. For example, the sections of the sleeve similar to Kamaena delicata originate both in the case of double-row and of composite verticils. The porosity of wall, observable in thin sections, corresponds at most with the less important and hypothetical 2nd order ramifications, while the 1st order branches have been left imperceptible in thin sections. Finally, the shape of partitions is probably more dependent on the mode of preservation and the way of neomorphism, than on the real differences in the structure of algae.

In this situation, a dozen or so genera and a great number of species distinguished on the basis of thin sections within the tribe Palaeobereselleae, seem to be a distinct overstatement. Naturally, a great taxonomical variety of these algae is not excluded, but verification of this is possible only when the specimens prepared from the rocks are obtained. The material described in this paper allows to recognize at least 3 genera with different types of verticils, and the hitherto existed descriptions of the palaeoberesellids point to the other next possibilities. For example, the genus Tringulinella MAMET, 1985, is characterized by a triangular shape of perpendicular section of the tube. By analogy to the other Carboniferous Dasycladaceae (e.g. above mentioned genus Kulikia), it seems probable that this original feature is caused by a metaspondyl arrangement of ramifications (3 clusters in each verticil). It is also probable that in the case of a higher frequency of specimens, it will be possible to find statistical relation between thin sections and three--dimensional specimens.

The next question refers to the position of the herein reconstructed Palaeobereselleae in the hitherto existing classifications. Homologies in the structure of the palaeoberesellids and the tribe Bereselleae are still veritable, in spite of new reconstruction of the former group. They differ surely by the type of branches, which are thinner in the tribe Bereselleae. BASSOULLET & al. (1979) excluded the both group from the order Dasycladales, although HERAK & al. (1977) connected with the Bereselleae (among others) an important stage of evolution in this very order (3rd stage, appearance of verticils). The Palaeobereselleae and Bereselleae are thereby similar to forms of such taxa as the genera Nanopora and Oligoporella, but they distinctly differ by their type of calcification realized around the verticils. For that reasons it seems necessary to unit the both groups in the form of a separate tribe within the order Dasycladales.

ECOLOGICAL IMPLICATIONS

Interpretative importance of the palaeoberesellids has considerably increased by confirmation of the dasycladacean nature of these microfossils. Bathymetrical range of Recent Dasycladales is relatively small, as usually these algae occur in masses not deeper than 30 m, although sporadically they exist to the 90 m (FLÜGEL 1985).

Abundant remains of the palaeoberesellid algae occur in shallow--water, near-subtidal environments of Devonian and Carboniferous epiplatform seas, in association with the other skeletal elements of similar bathymetrical limitations (cf. DREESEN & al. 1985, HENNEBERT & HANCE 1980, SKOMPSKI 1986, CHUVASHOV & RIDING 1984). Their value is greater in sediments significantly dominated by the Palaeobereselleae or in such deposits in which they are sporadic (e.g. of hypersaline or brackish waters).

The presence of the palaeoberesellids (Kamaena-like forms) is also recorded from the Waulsortian buildups in Western Europe regarded as deep-water (see LEES & al. 1977). Bathymetry of these enigmatic mud--mounds is still a subject of discussion, but in general the initiations of growth of the Waulsortian buildups took place at subphotic depths, probably exceeding 300 m (LEES & al. 1985). Such depths are estimated on the basis of approximated lower limits of the calcareous algae, micritization, plurilocular foraminifers and hyalostellid sponges. The palaeoberesellids appeared in the phase B and C of buildups growth, which were still connected with the subphotic zone (depth 200-300 m according to LEES & al. 1985; see also LEES & MILLER 1985, Fig. 8). Recognition of dasycladacean nature of the palaeoberesellid algae offers a different interpretation of the Waulsortian mud-mounds, which are thought to have probably originated in shallower environments.

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DAZYKLADOWATA NATURA PÓŹNOPALEOZOICZNYCH GLONÓW Z PODRODZINY PALAEOBERESELLEAE

(Streszczenie)

Przedmiotem pracy* jest analiza budowy glonów wapiennych z podrodziny Palaeobereselleae MAMET & ROUX, 1974, zachowanych w wyjątkowym stanie ośródek, a wypreparowanych z dolnokarbońskich wapieni Lubelskiego Zagłębia Węglowego oraz Sudetów. Te problematyczne mikroskamieniałości, znane dotychczas ze szlifów (*patrz* pl. 1—2), zaliczane były nie tylko do glonów, ale również do otwornic, a nawet gąbek. Porównanie morfologii ośródek (*patrz* pl. 3—6) i przekrojów otaczających je wapiennych osłonek wskazuje wyraźne podobieństwa budowy przedstawicieli podrodziny Palaeobereselleae do glonów wapiennych z rzędu Dasycładales (*patrz* fig. 1—2). Sprecyzowanie taksonomicznej pozycji paleobereselli zwiększa ich znaczenie przy analizie środowiska sedymentacji, powodując np. istotne zmiany dotychczasowych wnioskowań paleobatymetrycznych, co zaprezentowano na przykładzie facji Waulsortian z dolnego karbonu Europy Zachodniej.

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