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Upper Jurassic bacteria from the Raptawicka Turnia Limestone Formation in the Mały Giewont area (Western Tatra Mountains, Poland)

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Fossil filamentous and non-filamentous bacteria are reported from the Upper Jurassic limestones of the Raptawicka Turnia Limestone Formation in the Mały Giewont sections of the Western Tatra Mountains (Poland). The filamentous bacteria are subdivided into five groups: thin uniseriate, large multi-cell, large spiral, tapering and branched forms. The thin uniseriate filaments are the main microbial component of the peloids and micro-oncoids from the studied formation, mainly in the Upper Kimmeridgian–Tithonian limestones. The presence of the heterocyte-like terminal cells suggests their interpretation as cyanobacteria similar to the modern order Nostocales and perhaps to the family Nostocaceae. The large multi-cell and tapering filaments are uncommon in the studied limestones. The branched filaments found in the Tithonian limestones, although thinner, probably also may be compared with some modern representatives of the order Nostocales. Non-filamentous fossil bacteria found in the studied limestones consist of rod-shaped bacilli, monotrichous bacilli and spirilla; they belong mainly to the phylum Proteobacteria. Some microborings observed in the microfossils occurring in the micro-oncoids remind the ichnotaxon *Scolecia filosa* Radtke known to be of wide palaeobathymetric range. The thinnest microborings resemble another group of ichnofossils named "Pygmy form", probably also of bacterial origin. The Upper Kimmeridgian–Tithonian micro-oncoids were formed mainly by filamentous bacteria (Cyanobacteria) that overgrew successively their nuclei with a few to several laminae. Frequent occurrence of pelagic microfossils as nuclei of micro-oncoids does not match a transport of these coated grains from much shallower sedimentary environments. The fossil filamentous bacteria filling up the peloids and micro-oncoids could be adapted to conditions that existed in the sublittoral zone below the wave base.

Key words: fossil bacteria, micro-oncoids, Kimmeridgian–Tithonian, Tatra Mountains.

INTRODUCTION AND PREVIOUS RESEARCH

The pelagic "oolites" as defined by Jenkyns (1972) were considered to represent a distinctive lithology of the Tethyan Upper Jurassic (Jenkyns, 1980). Earlier, Lefeld and Radwański (1960) postulated that the "pseudo-ooids" (= micro-oncoids and peloids) from the Upper Jurassic and Lower Cretaceous limestones of the High-Tatric Succession (Tatra Mountains, southern Poland – Fig. 1) formed probably as a result of activity of Cyanophyceae (now Cyanobacteria). Their interpretation was not supported with any direct evidence, as at that time the fossil microbial structures could not be documented with the appropriate light microscopic (LM) photographs nor scanning electron microscopic images (SEM photomicrographs). Jenkyns (1972) concluded that micro-oncoids from the Upper Jurassic limestones were linked with sedimentation in the photic zone under pelagic conditions. Jenkyns (1972) agreed with the opinion of Lefeld and Radwański (1960) about the cyanophycean origin of their "pseudo-ooids", but also his figures did not show any direct evidence of the presence of the microbial fossils in micro-oncoids and peloids. According to Mišik (1998: 15), "It cannot be excluded that the 'pelagic' micro-oncoids were produced by bacterial activity under the photic zone and the sorting of micro-oncoids was carried out by bottom currents". Probably, the first documentation on the occurrence of microbial filaments was recently presented for a Lower Kimmeridgian peloid and two Tithonian coated grains (Pszczółkowski et al., 2016).

The main objectives of the present contribution are as follows: (1) to describe and illustrate fossil bacteria from the Upper Jurassic limestones of the Mały Giewont area (High-Tatric Succession), mainly those occurring in micro-oncoids and peloids, and (2) to indicate their probable systematic affinity by comparison of their morphology mainly with the modern taxa of bacteria.

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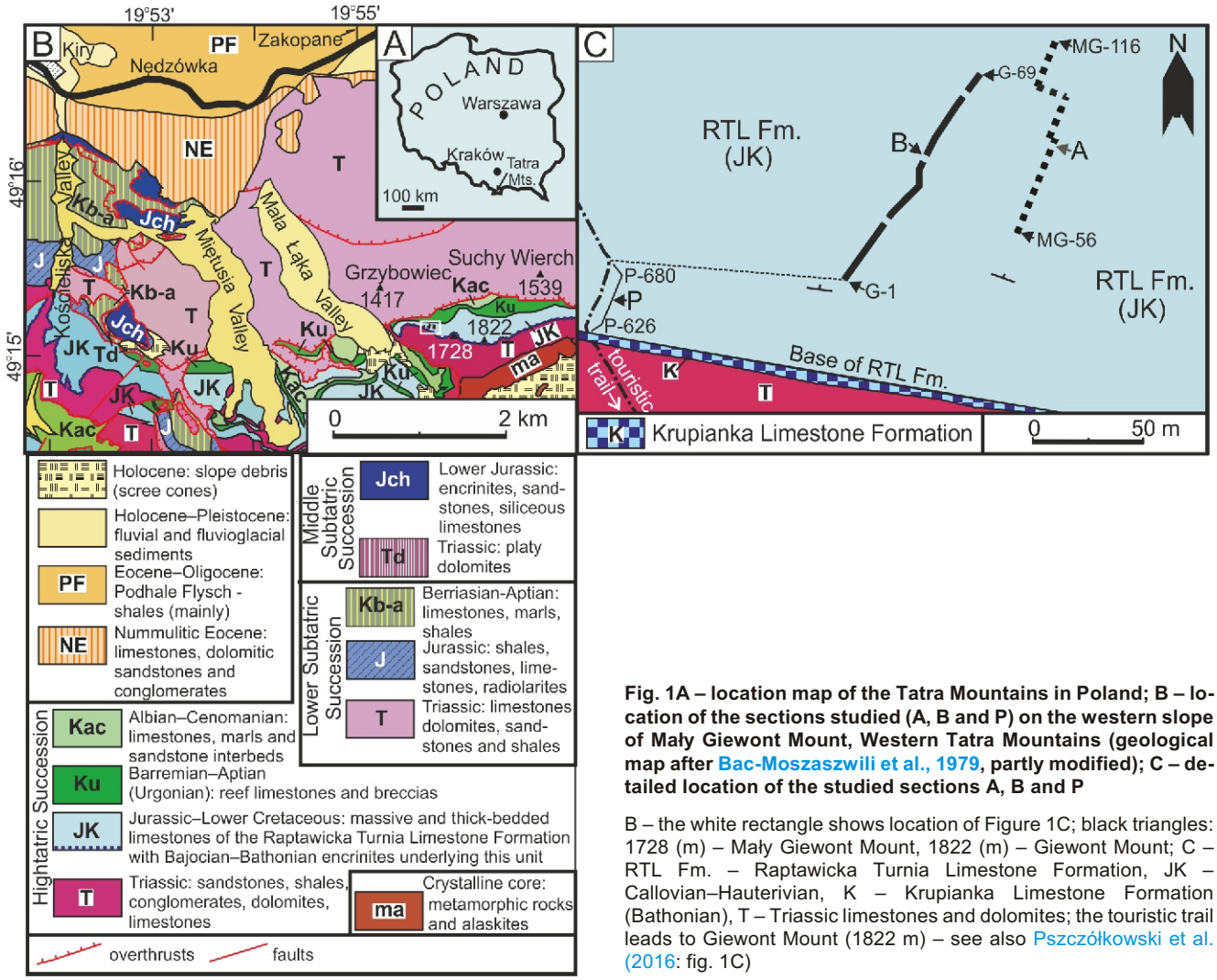


Fig. 1A – location map of the Tatra Mountains in Poland; B – location of the sections studied (A, B and P) on the western slope of Mały Giewont Mount, Western Tatra Mountains (geological map after Bac-Moszaszwili et al., 1979, partly modified); C – detailed location of the studied sections A, B and P

B – the white rectangle shows location of Figure 1C; black triangles: 1728 (m) – Mały Giewont Mount, 1822 (m) – Giewont Mount; C – RTL Fm. – Raptawicka Turnia Limestone Formation, JK – Callovian–Hauterivian, K – Krupianka Limestone Formation (Bathonian), T – Triassic limestones and dolomites; the touristic trail leads to Giewont Mount (1822 m) – see also Pszczółkowski et al. (2016: fig. 1C)

MATERIAL AND METHODS

The samples for this study were collected from three sections of the Raptawicka Turnia Limestone Formation (RTL Fm.) located at the western slope of Mały Giewont Mount, Western Tatra Mountains in Poland (Fig. 1; see also Pszczółkowski et al., 2016). Fifty-six samples were taken from section A, 69 from section B, and 54 from section P. The microbial fossils were studied in thin-sections with a *Nikon Polarizing Microscope ECLIPSE LV100POL* at the Institute of Geological Sciences (Research Centre in Warsaw), Polish Academy of Sciences. The microbial fabric of the peloids and micro-oncoids from the RTL Fm. in Mały Giewont was investigated in thin-sections under a light microscope (LM); magnification ~1000X reveals the dense meshwork of thin calcified filaments. Further enlargement of the LM photographs (or its fragments) up to ~2800X allows to discern details of these filaments. Six samples of limestones from sections B and P were investigated under a scanning electron microscope (SEM) *JEOL JSM/JXM 840A*, also at the Research Centre in Warsaw of the Institute of Geological Sciences.

GEOLOGICAL SETTING

Lefeld (in Lefeld et al., 1985: 26–30) included the Upper Jurassic and Lower Cretaceous limestones of the High-Tatric Succession in the Raptawicka Turnia Limestone Formation. One of the reference sections of this formation was designated on the western slope of Mały Giewont Mount in the Western Tatra Mountains (Lefeld et al., 1985: 26, fig. 7). The Upper Jurassic limestones of the Raptawicka Turnia Limestone Formation (RTL Fm.) were sampled on the northwestern slope of Mały Giewont Mount along three sections: A, B and P in Figure 1B, C (see also Pszczółkowski et al., 2016). Section A, located in the middle of the northwestern slope of Mały Giewont Mount (Fig. 1B, C), comprises Kimmeridgian–Tithonian limestones of the RTL Fm., 65 m thick (Fig. 2). Section B is placed 55 m west and downslope of section A (Fig. 1B, C); its base (sample G-1) is located 32 m above the lower boundary of the RTL Fm. (Fig. 1C). The sampled beds of section B are composed of the Kimmeridgian–Tithonian limestones, 67 m thick (Fig. 2, section B). Section P is exposed along a tourist trail leading to Giewont Mount (Fig. 1C); 55 samples (P-626 to P-680) were collected from the Callovian–Lower Kimmeridgian limestones (Fig. 2, sections B and P).

Macrofauna is scarce in the Upper Jurassic limestones of the RTL Fm. (Passendorfer, 1928, 1951). The biostratigraphical subdivision of these limestones exposed on the western slope of Mały Giewont Mount is based mainly on planktic microfossils (calcareous dinoflagellate cysts, chitinoidellids and calpionellids; Pszczółkowski et al., 2016).

In the Mały Giewont sections, the following microfossil zones were distinguished in the studied limestones of the RTL Fm.: *acme* Fibrata (Oxfordian), *acme* Parvula (Lower Kimmeridgian), Moluccana, Borzai (Upper Kimmeridgian),

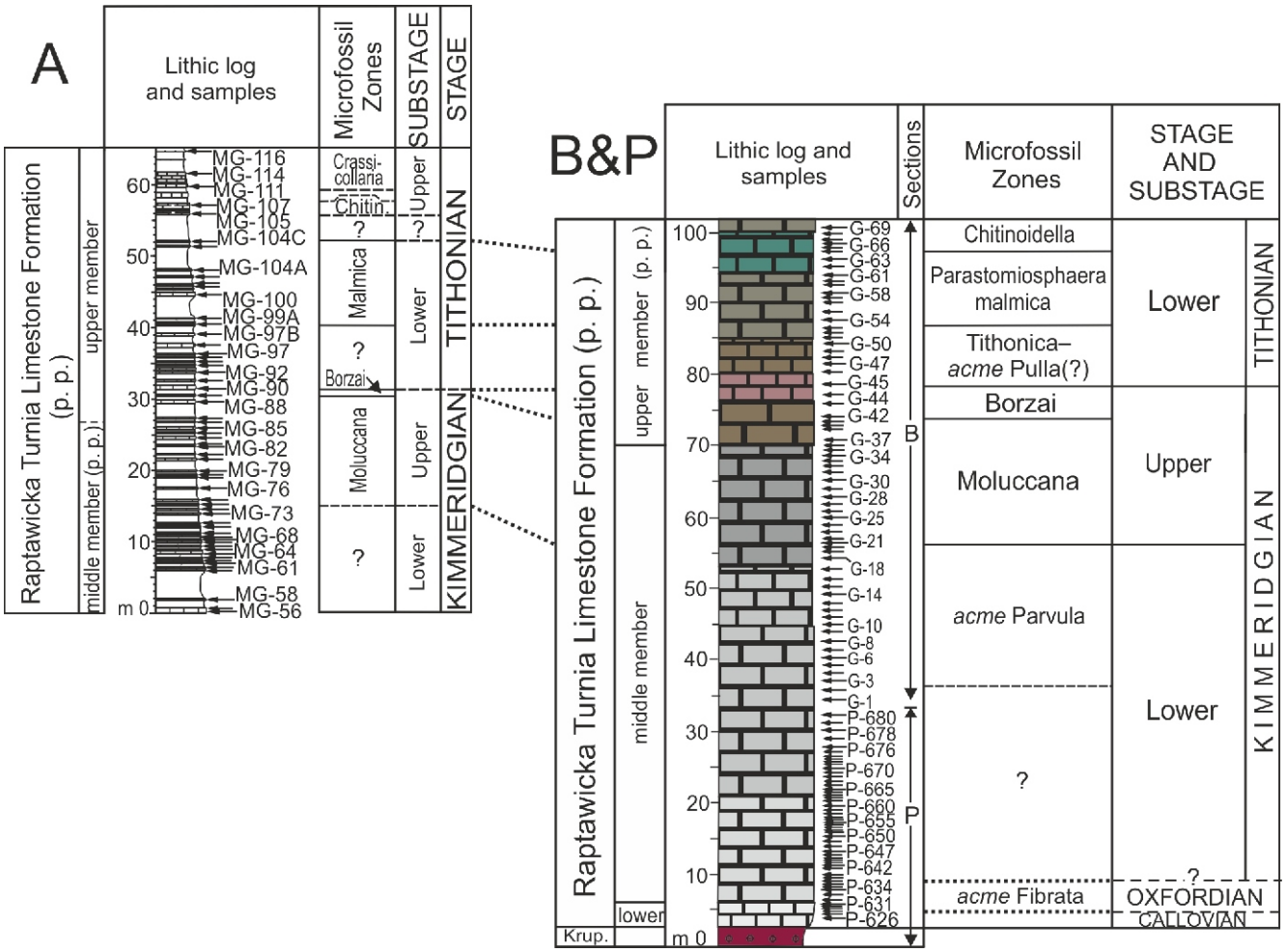


Fig. 2. Sections A, B and P exposed on the western slope of Mały Giewont Mount, Western Tatra Mountains (Fig. 1B, C; after Pszczółkowski et al., 2016: fig. 4, partly modified)

Krup. – Krupianka Limestone Formation (Bathonian after Lefeld in Lefeld et al., 1985: 24–25), Chitin. – Chitinoidella Zone (section A); dotted lines between the sections indicate correlation of the microfossil zones

Tithonica-*acme* Pulla(?), Malmica (Lower Tithonian), Chitinoidella and Crassicollaria (Lower–Upper Tithonian, Fig. 2; see also Pszczółkowski et al., 2016). The Upper Tithonian Crassicollaria Zone (*pro parte*) was reported only from section A (Fig. 2). The limestones, ~25 m thick, between the *acme* Fibrata and *acme* Parvula zones were studied in section P only (Fig. 2). Infrequent calcareous dinocysts do occur in this interval (*Schizosphaerella* cf. *minutissima* and *Colomisphaera* cf. *lapidosa*), but the taxa indicative of the zones established for the Carpathians (Reháková, 2000; Reháková et al., 2011; Jach et al., 2014) were not recorded. The *Globochaete* microfacies is characteristic for these Lower Kimmeridgian limestones. In section B (Fig. 2), the following microfacies occur (Pszczółkowski et al., 2016): *Bositra* (Callovian), *Conoglobigerina* (Oxfordian), *Globochaete* (Upper Oxfordian–Lower Kimmeridgian), *Globochaete*—Saccocomidae (Lower Kimmeridgian), *Bositra*–Saccocomidae (Lower–Upper Kimmeridgian), *Saccocoma*–*Globochaete* (Upper Kimmeridgian–Lower Tithonian) and *Saccocoma* (Tithonian). Peloids predominate in the *Globochaete* MF, whereas micro-oncoids and cortoids are common in the last three microfacies types. In section A (Fig. 2), the Kimmeridgian–Tithonian limestones contain three microfacies: *Globochaete*–Saccocomidae, *Bositra*–Saccocomidae (or its variant, *Bositra*–Saccocomidae–*Globochaete*) and *Saccocoma*–*Globochaete* (Pszczółkowski et al., 2016).

RESULTS

PELOIDS AND MICRO-ONCOIDS

The peloids and micro-oncoids are ubiquitous in the Upper Jurassic limestones of the Raptawicka Turnia Limestone Formation. The peloids are 40–600 μm in diameter being usually darker than the surrounding deposit or cement (Figs. 3A, 4F, 5A, 6A and 7E). Some Upper Kimmeridgian–Tithonian peloids are composed mainly of microbial filaments (Figs. 3A, C and 6A, B), with a subordinate admixture of other components, such as calcareous nannofossils and micrite. Such grains can correspond to algal and microbial (cyanobacterial) peloids or pellets (Flügel, 2004). However, in the Lower Kimmeridgian limestones, there are peloids consisting of micritic matrix with dispersed microbial filaments (Pszczółkowski et al., 2016: fig. 5B) or displaying partly recrystallized structure (Fig. 5A) with a few microbial filaments and calcareous nannofossils (Fig. 5C). In general, some peloids from the Upper Jurassic limestones of the RTL Fm. may represent faecal pellets – oval or elongate, sometimes spindle-shaped.

In the studied limestones, the micro-oncoids are 0.2–1.0 mm in diameter; their cortices are composed of layers (laminae) usually 10–40 μm wide. The laminae are typically regular in shape and usually do not overlap. The bright layers are

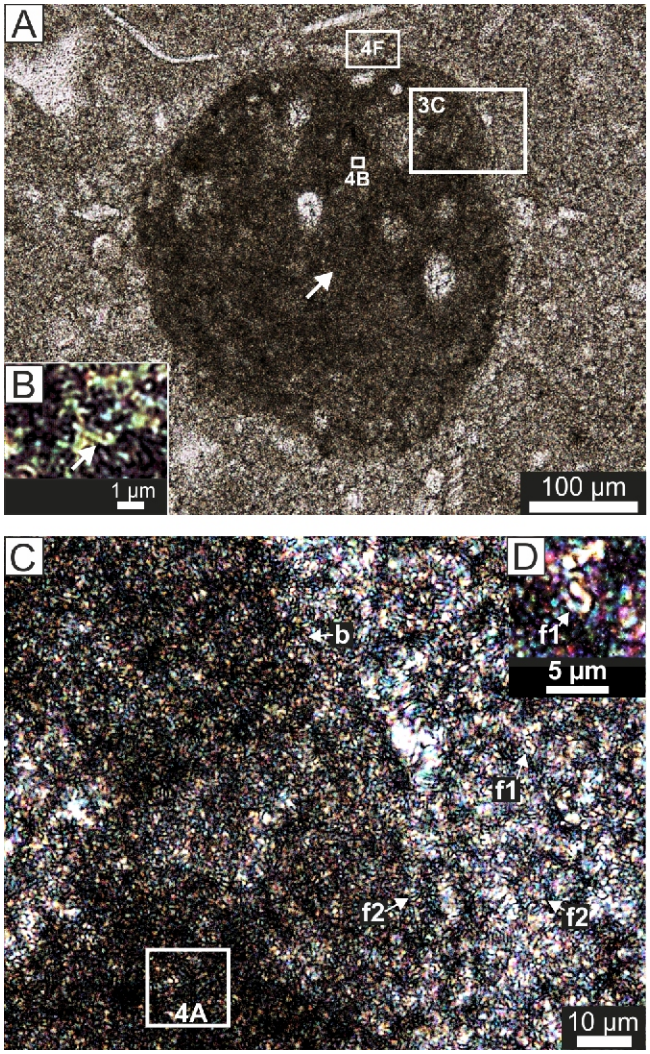


Fig. 3A – dark peloid, 380 µm in diameter, composed mainly of densely packed uniseriate microbial filaments, 0.3–1.0 µm wide, straight or irregularly curved (sample/thin-section G-40, section B in Fig. 2, uppermost Kimmeridgian), white rectangles denote fragments shown in Figures 3C and 4B, F, arrow indicates location of bacterium illustrated in Figure 3B, in the central part of the peloid; B – rod-shaped bacterium (arrow) 0.2 µm wide and 1.7 µm long; C – enlarged part of Figure 3A showing fragment of peloid illustrated in Figure 3A (on the left) and bacteria-bearing deposit (biomicrite, on the right): (b) bacterium with polar flagella in the marginal part of the peloid (see also Fig. 11A), (f1) planispiral microbial filament located in the deposit outside the peloid (cf. Fig. 3D), (f2) bundles of uniseriate filaments, 6 and 7 µm in diameter, in the marginal zone of the peloid and in the deposit, rectangle indicates location of the peloid fragment shown in Figure 4A; D – enlarged part of Figure 3C showing planispiral microbial filament (f1) composed of 8 to 9 segments (probably fossilized cells) with the larger apical one (0.9 µm wide)

more resistant forming apparent "ridges" in the LM view of thin-section, whereas the dark layers seem to occur as tiny concentric "depressions" (Figs. 7A, 8A, 10A and 12A). This contrast between the laminae is probably related to fluctuations in $CaCO_3$ content. The microbial filaments are perpendicular to the – rather diffuse – concentric layers' borders ("erect cyanobacterial filaments" – Riding, 1991), but sometimes their orientation seems to be quite irregular inside the laminae. The nuclei of micro-oncoids contain commonly pelagic microfossils (Figs. 8A and 12A), but benthic foraminifera are also present (Pszczółkowski et al., 2016). The white fine-grained calcium carbonate infilling the central part of the microfossil, occurring as the nucleus of the micro-oncoid (Fig. 8B), is composed of clots, about 0.25 µm across. This clotted fabric (cf. Riding, 2000) seems to pass into dense micrite (Amorphous Calcium Carbonate? – ACC, cf. Weiner et al., 2003).

INFORMAL GROUPS OF MICROBIAL FOSSILS

MICROBIAL FILAMENTS

1. **Thin uniseriate filaments**. The microbial fossils frequently observed in the Upper Jurassic limestones of the Mały Giewont sections are thin uniseriate multi-cell calcified filaments occurring in the micro-oncoids and peloids, but sometimes also outside these grains in the surrounding deposit. These filaments are straight or curved, sometimes nearly planispiral (Fig. 3D), up to 20 µm in length. Transverse sections of the filaments are 0.2–1.0 µm wide (Fig. 4C, E, F); however, the diameter of their terminal (apical) cells can range from ~0.8 up to 2.4 µm (tc in Figs. 4C, E and 7C, D). The peloids from the Oxfordian–Lower Kimmeridgian limestones contain thin uniseriate microbial filaments, sometimes hardly visible in the micritic matrix (Pszczółkowski et al., 2016: fig. 5B) or within a pseudo-radial fabric of these grains (this study, Fig. 5A). Individual microbial filaments from the Lower Kimmeridgian limestones are composed of a calcified sheath, 0.25 µm thick, and a hollow central part – probably after degraded trichome (Fig. 5E). The partitions marked on the calcified sheath possibly represent the traces of walls between the trichome cells (Fig. 5E). The calcified sheath is composed of very fine-grained (amorphous?) calcium carbonate.

The peloids from the Upper Kimmeridgian–Tithonian limestones are usually composed of densely packed thin microbial filaments (f1 in the upper right part of Fig. 6B), sometimes dichotomously branched (f2 in Fig. 6B). However, systematic identity of the branched filaments and the uniseriate ones is uncertain. Some uniseriate filaments are composed of 6 to 9 cells (f1 in Figs. 3C, D; f in Figs. 4E and 7C). The calcified filaments can form circular or oval bundles, 5–17 µm in diameter, in peloids (f2 in Fig. 3C; f1 in the central part of Fig. 6B; f in Fig. 7D) and micro-oncoids (fb in Fig. 7B and f1 in Fig. 10C), as well as in the surrounding biomicrite (f2 in Fig. 3C, on the right; fb in Fig. 4F). The filament bundle (f1) shown in Figure 10C resembles an overturned basket, about 3 µm in diameter at the base, 5 µm at the top, and 3.5 µm high.

The thin uniseriate microbial filaments are frequently terminated with cone-shaped cells (tc in Fig. 4C, E) or, sometimes, with smaller dark ovoid cells (f1 in the lower left part of Fig. 6B). Some filaments are terminated with larger spindle-form cells (tc in Fig. 7C, D – in the lower part of the image). The results of LM analysis show that the above-described fossil uniseriate filaments are the main – although not unique (see below) – microbial component of the peloids and micro-oncoids from the studied limestones of the RTL Fm., mainly in the Late Kimmeridgian–Tithonian strata.

The Upper Kimmeridgian dark uniseriate filament shown as f1 in Figure 11C is ~1 µm wide and 6 µm long. The filament seems to occur within a larger microboring cut by a thin-section plane. In an Upper Tithonian micro-oncoid (Fig. 8A) the straight filaments (5–10 0.3–0.6 µm), terminated with slightly larger cone-shaped or oval elongate cells, also occur in microborings (f in Fig. 8B). Their palaeoecological status and

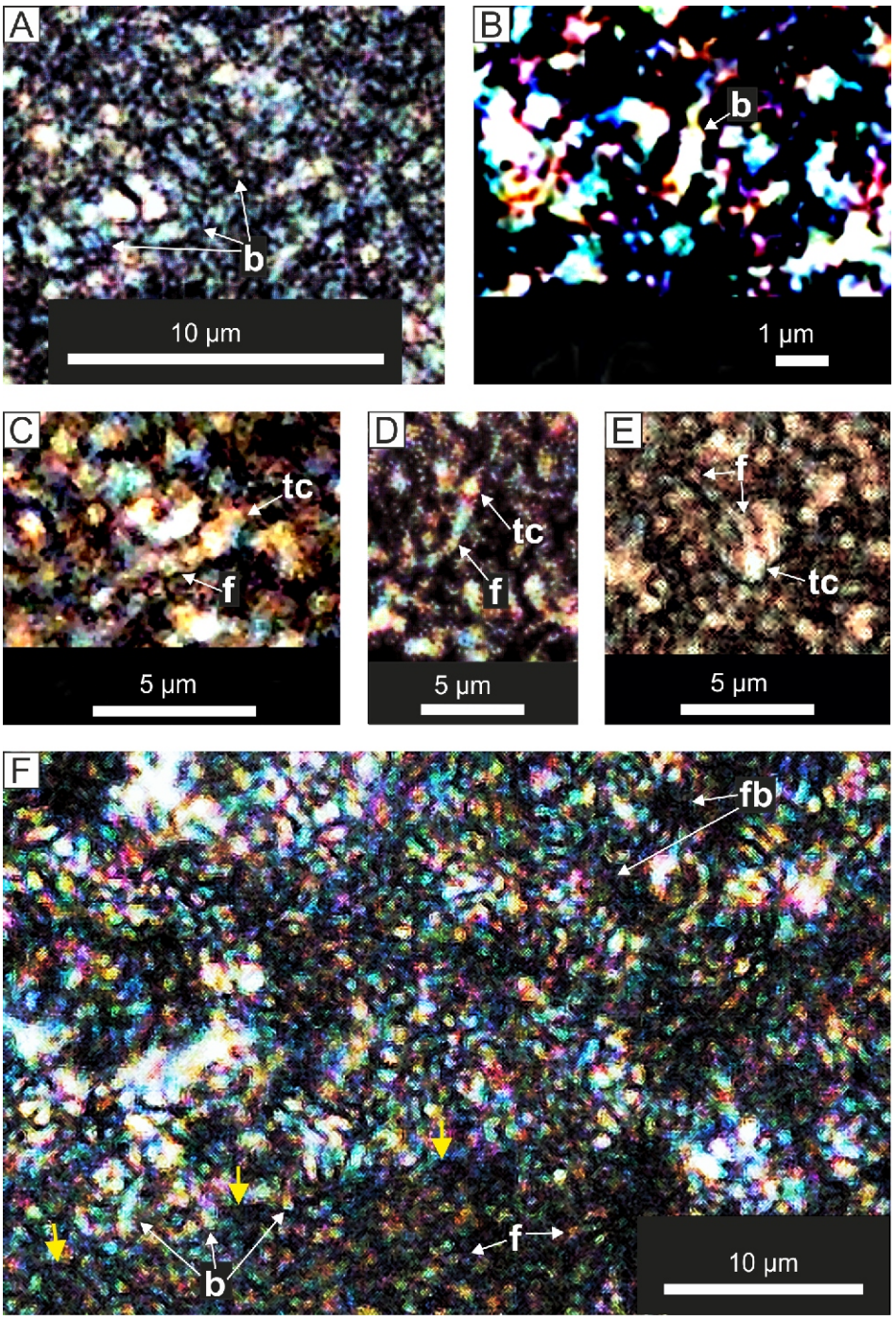


Fig. 4. Fossil microbial forms in peloids and micro-oncoids (crossed polars)

A – enlarged part of the peloid shown in Figure 3C – (b) helicoid bacteria, 0.2 μm in diameter and 2 μm long; **B** – enlarged part of the peloid illustrated in Figure 3A – (b) cylindrical bacterium, 0.5 μm wide and 1.4 μm long, terminated with thinner screw-like flagellum; **C** – microbial filament (f) composed of 5(?) segments and a larger (elongate) terminal cell (tc), sample G-26, Upper Kimmeridgian; **D** – microbial filament (f) consisting of a few segments and a larger cone-shaped terminal cell (tc), occurring in a micro-oncoid (sample/thin-section G-68, section B in Fig. 2, Chitinoidella Zone, Tithonian), crossed polars; **E** – microbial filament, 4.7 0.6 μm (f), terminated with a larger cell, 1.2 μm wide (tc), in a micro-oncoid (sample/thin-section G-27, biooncomicrite, section B in Fig. 2, Moluccana Zone, Upper Kimmeridgian), crossed polars; **F** – enlarged part of Figure 3A – yellow arrows in the lower part of the image indicate the boundary of the dark peloid, (b) monotrichous bacteria, 0.5–0.9 μm wide, (f) thin microbial filaments (0.4–0.6 μm wide) occurring in the peloid, some terminated with a larger cell, 0.7 –1.0 μm in diameter, (fb) filament bundles, 4 and 9.5 μm in diameter, visible in the deposit

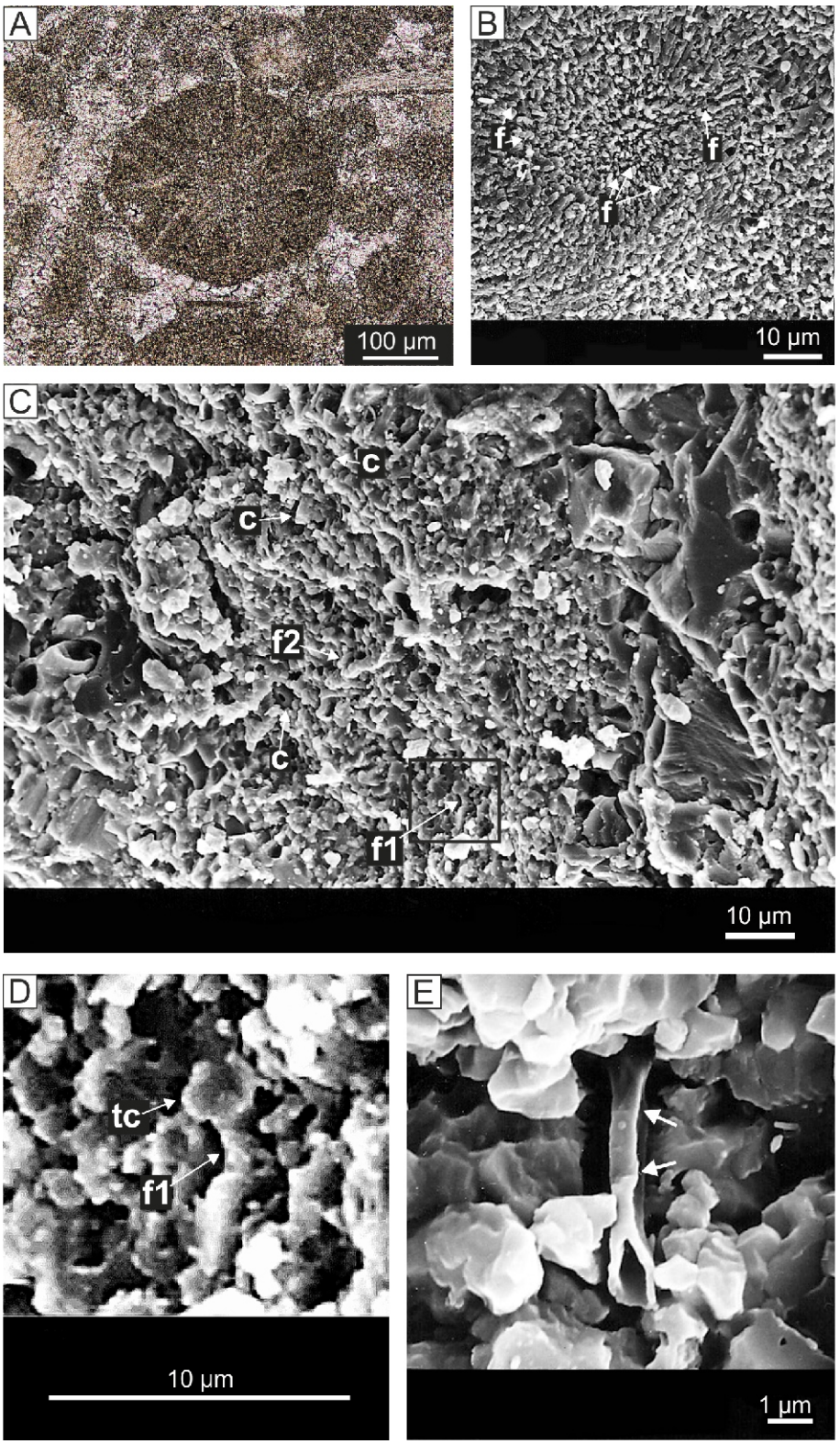


Fig. 5. Lower Kimmeridgian microbial filaments and nannofossils in peloids

A – peloid (310 µm in diameter) with a pseudoradial structure, thin uniseriate microbial filaments between the calcitic "rays" can be recognized under higher magnification (G-13, section B in Fig. 2); **B** – SEM photomicrograph of a radial ooid with a peloid as a nucleus composed mainly of microbial filaments, 0.2–0.6 µm wide, and a few micrometres long (f), sample/thin-section P-642, limestone chip etched in 3% HCl (section P in Fig. 2, lowermost Kimmeridgian); **C** – SEM photomicrograph of a small peloid (64 52 µm) containing a few microbial filaments terminated with a cup-shaped (f1) or globular cell (f2) and calcareous nannofossils (c), rectangle indicates the part enlarged in Figure 5D (sample/thin-section P-642, section P in Fig. 2, Lower Kimmeridgian); **D** – enlarged part of Figure 5C: (f1) microbial filament with minor branches, (tc) terminal cup-shaped cell; **E** – SEM photomicrograph of a tube-like microbial form (filament), 0.7–1.0 µm in diameter, the wall is 0.25 µm thick, arrows indicate boundaries of tube segments (cells?), fresh chip (sample/thin-section P-642, section P in Fig. 2, Lower Kimmeridgian)

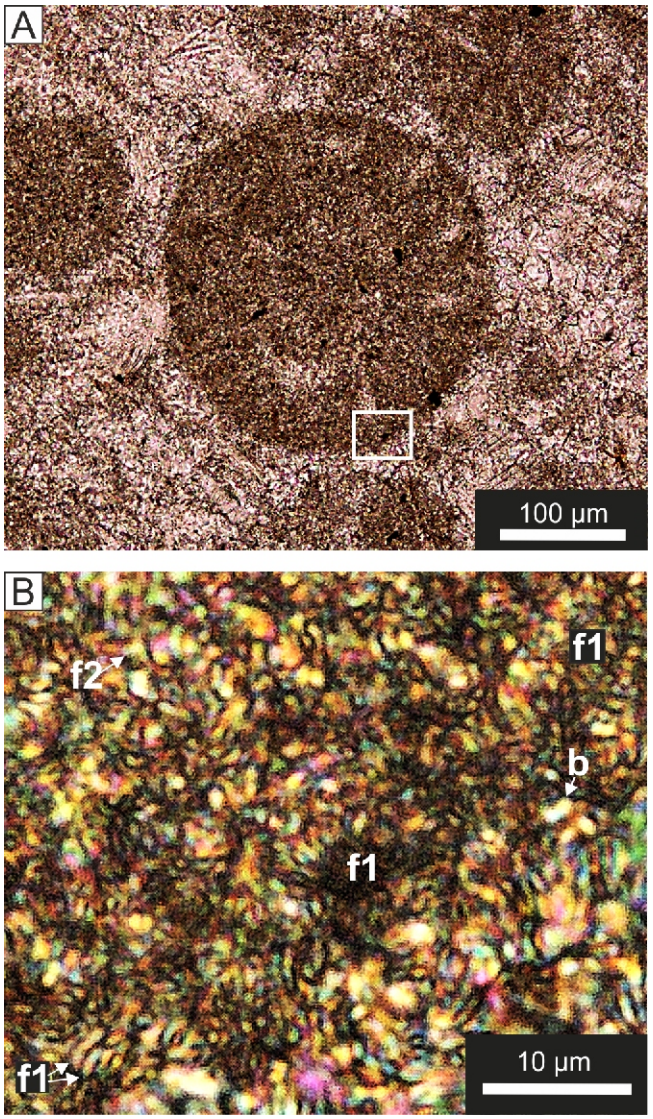


Fig. 6A – peloid (273 µm in diameter) showing a spongy structure with numerous microbial filaments, rectangle indicates location of the part displayed in Figure 6B (thin-section G-27, section B in Fig. 2, Moluccana Zone, Upper Kimmeridgian); B – (f1) uniseriate microbial filaments, 0.4–0.8 µm wide, some terminated with smaller dark cells (lower left) similar to heterocytes of some modern cyanobacteria; the filaments form in places circular bundles (centre) or dense thicket (upper right), (f2) dichotomously branched filament, (b) rod-shaped bacterium (2.0 1.0 µm) supported with several short (lateral) tubular appendages (crossed polars)

taxonomic position may be different in comparison with the other (above described) thin uniserial filaments (f2 in Fig. 11C).

2. **A large multi-cell filament**. A microbial filament (f in Fig. 9A), 10 µm long and 1.6 µm wide, was found in the Upper Kimmeridgian limestone (sample/thin-section G-27, section B in Fig. 2). The filament is terminated with a conical cell (tc in Fig. 9A). This type of microbial filaments is by far less frequent in the studied limestones than the thinner form.

3. **A large spiral filament**. A relatively large spiral microbial filament (~13 1.8 µm) was detected in a Tithonian micro-oncoid from the Chitinoidella Zone (Fig. 9D, E). Similar filaments occur also in the Upper Tithonian micro-oncoid (Fig. 10A, A').

4. **Tapering filaments**. Microbial filaments tapering from one end to the other (Fig. 9C, G) occur in the Tithonian limestones; their dimensions are 5.5 0.8–1.5 µm and 4.5 0.9–2 µm, respectively. The smaller filament shown in Figure 4D (4.0 µm long and up to 0.7 µm wide) also belongs to this group. The filaments shown in Figure 9C, G have a button-like cell at the thinner end (h), which resembles a holdfast.

5. **Branched filaments**. The following examples are illustrated: (a) a microbial filament labelled f1 in Figure 5C, D with minor lateral branches and terminal cup-shaped cell (tc – apical one or holdfast?) from the Lower Kimmeridgian peloid, (b) a microbial filament (f) with minor lateral branches and a globular terminal cell (tc in Fig. 7G) in the marginal part of a peloid from the Tithonian Chitinoidella Zone (Fig. 7E), (c) branched microbial filaments in micro-oncoids from the Tithonian limestones (f in Figs. 9I and 10B; f2 ithin-sectionn Fig. 10C), and (d) branched microbial filaments, 0.2–0.7 µm wide, from the peloid (faecal pellet?) in the Tithonian Chitinoidella Zone (Fig. 10D). As concerns the last example, the filaments are thin tubes with an empty central canal, ~0.2 µm in diameter; some filaments are terminated with larger apical cells (tc in Fig. 10D). In the Tithonian limestones, the branched filaments are the second important component of some peloids and micro-oncoids (after the thin uniseriate filaments).

NON-FILAMENTOUS BACTERIA

1. A rod-shaped bacterium, 1.7 0.2 µm, curved at one end occurs in the peloid from the uppermost Kimmeridgian limestone (Fig. 3A, B).

2. (a) The bacterium indicated in Figure 3C (b) and enlarged in Figure 11A occurs in the marginal part of the same Kimmeridgian peloid. A similar specimen is located not far from the above-indicated bacterium, also in the marginal zone of the peloid.

(b) Another bacterium from the same uppermost Kimmeridgian peloid is composed of a rod-shaped cell (1.4 0.5 µm) and one polar flagellum, ~1.7 µm in length (Fig. 4B). Similar bacteria occur in the Upper Kimmeridgian limestone (b in Fig. 4F) and in the Tithonian oncosparite (b1 in Fig. 7C). The specimen from the Tithonian Chitinoidella Zone (b in Fig. 9I), although strongly bent, probably also belongs to this group of bacteria.

3. A small bacterium (cell dimensions: 1.4 x 0.9 µm) supplied with a single polar flagellum (b in Fig. 9G and H) occurs in a Lower Tithonian micro-oncoid (Malmica Zone).

4. A rod-shaped cell (2.0 1.0 µm) with several short tubular appendages (b in Fig. 6B) is present in the Upper Kimmeridgian limestone; the bacterium is situated at the margin of the peloid shown in Figure 6A.

5. The Late Kimmeridgian (Moluccana Zone) rod-shaped bacterium, with tuft of flagella at one pole, has a cell 1.2 µm wide and 3 µm long (b in Fig. 9A).

6. A crescent-shaped bacterium (1.5 0.8 µm) with a single spiral flagellum, 2 µm long, is illustrated from an Upper Kimmeridgian peloid (b1 in Fig. 9B).

7. Spiral bacteria (spirilla) occur in some peloids from the uppermost Kimmeridgian (Fig. 4A) and Tithonian limestones (b2 in Fig. 7C and b in Fig. 7G). These bacteria form ring-shaped clockwise helices, 0.2 µm wide and 2.5 µm long (Fig. 7G). The larger spirilla (12 µm long and 1 µm in diameter – Fig. 7F) from the Tithonian Chitinoidella Zone and from the Lower Kimmeridgian limestone (5.1 0.3-0.6 µm – Fig. 9F) probably also belong to this bacterial group.

8. Subglobular cells with spiral flagellum (b2 in Fig. 7C and b in Fig. 7D) are rather difficult to study in thin-sections because

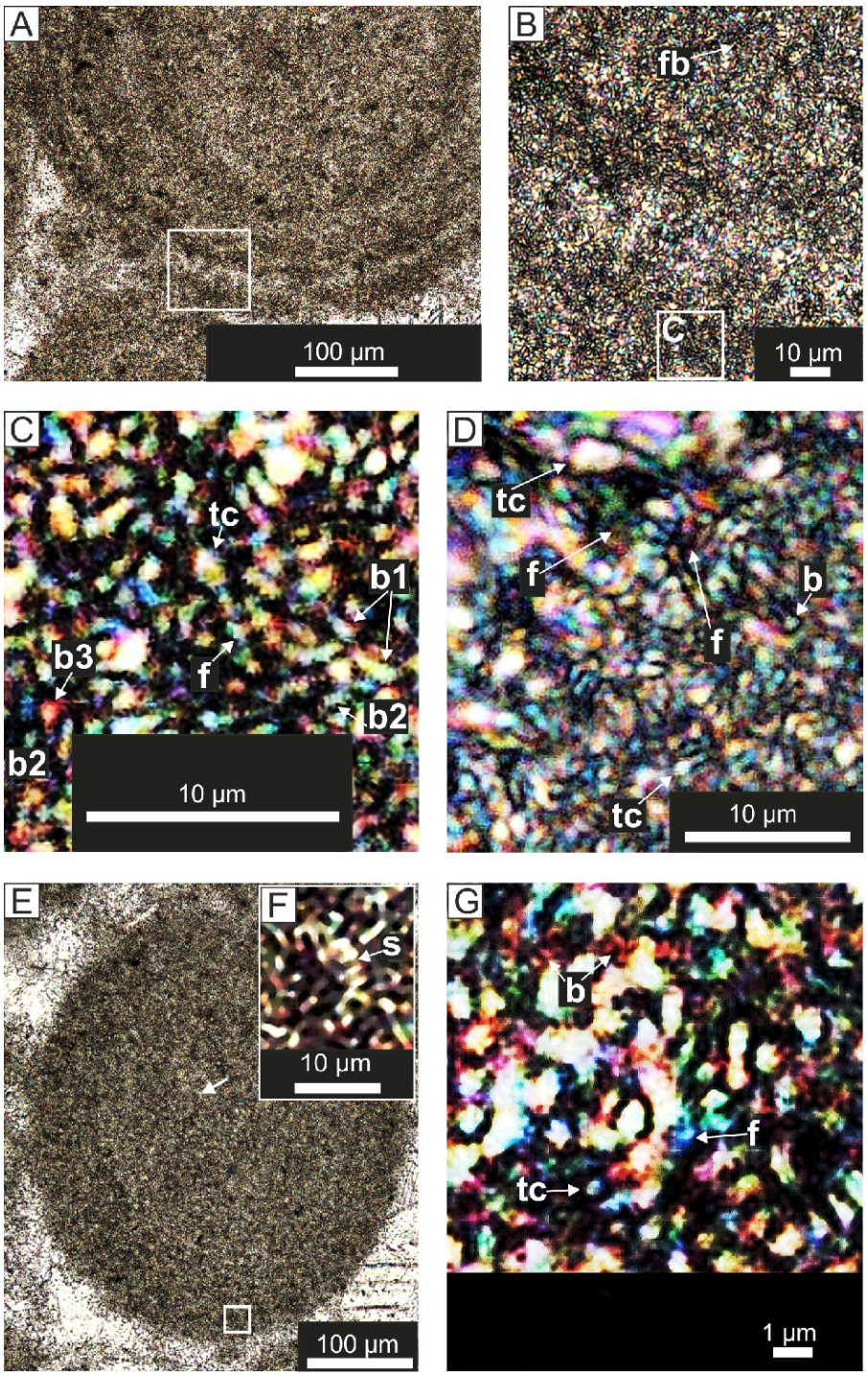


Fig. 7. Microbial filaments and non-filamentous bacteria from the Chitinoidella Zone, Tithonian

A – part of weakly developed micro-oncoid (~0.5 mm in diameter), rectangle indicates a fragment shown in Figure 7B (thin-section G-69, section B in Fig. 2); **B** – enlarged fragment of the micro-oncoid illustrated in Figure 7A: the photomicrograph shows microbial meshwork of the cortex and a bundle (about 17 µm in diameter) of uniseriate filaments (fb), individual filaments are 0.5–0.8 µm in diameter, rectangle denotes the area enlarged in Figure 7C; **C** – enlarged part of Figure 7B: (b1) rod-shaped monotrichous bacteria, (b2) thin spiral bacteria, (b3) small coccoid body with a polar flagellum, (f) straight filament, 0.6 µm wide, terminated with a larger apical cell (tc), crossed polars; **D** – (f) bundles (up to 7.5 µm in diameter) of microbial filaments in a peloid: (tc) larger apical cells of some microbial filaments, (b) small coccoid body with polar flagellum (sample/thin-section G-67, section B in Fig. 2), crossed polars; **E** – peloid, 407 µm in diameter, composed of uniseriate (and some bifurcated) microbial filaments up to 15 µm long, a spirillum visible in the central part of the peloid (arrow), enlarged in Figure 7F, rectangle indicates the area shown in Figure 7G (thin-section G-66, section B in Fig. 2); **F** – enlarged fragment of the central part of the peloid shown in Figure 7E: (s) spirillum 12 1 µm; **G** – microbial filaments located in the marginal zone of the peloid shown in Figure 7E (crossed polars): (f) filament, 4.7 µm long and 1.1 µm wide, with smaller offshoots and the globose terminal cell (tc), (b) spirilla, 2.5 µm long and ~0.2 µm wide, with hook-like ends

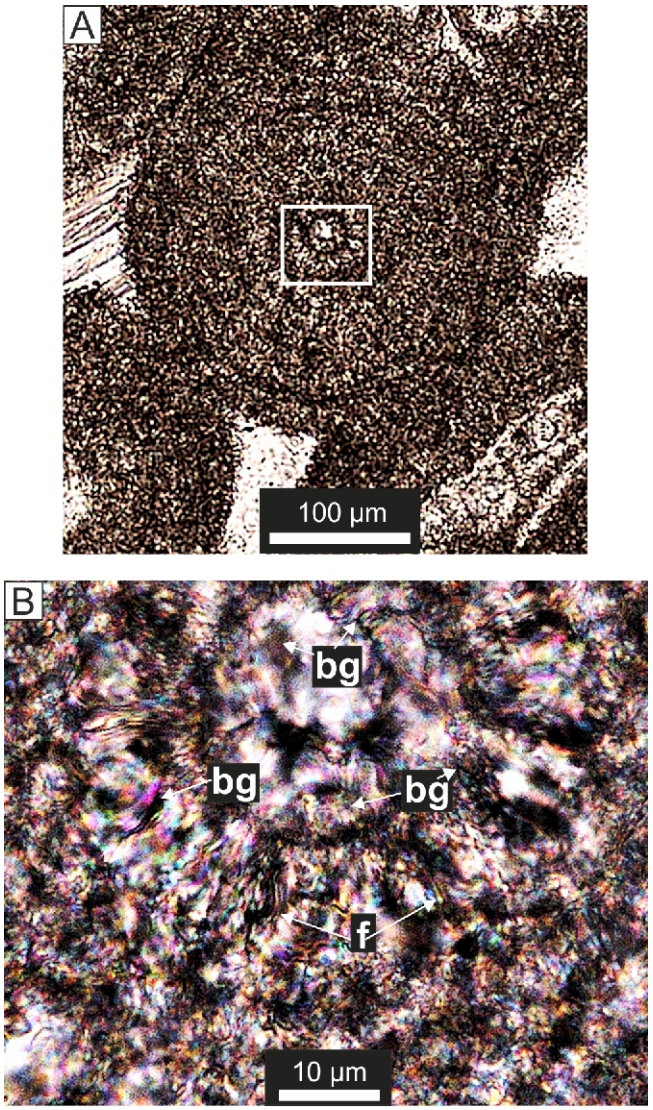


Fig. 8A – micro-oncoid with *Colomisphaera* cf. *carpathica* (Borza) as nucleus, rectangle indicates the part enlarged in Figure 8B (thin-section MG-113, section A in Fig. 2, Crassicollaria Zone, Upper Tithonian); B – enlarged part of Figure 8A: (bg) microborings of microbial endoliths (the thinnest borings are 0.2–0.3 µm in diameter), (f) uniseriate microbial filaments (5–10 0.3–0.5 µm) occurring in the microborings within the wall of a calcareous dinoflagellate cyst (crossed polars)

of their small dimensions (cell 0.8 µm wide, flagellum ~1 µm long – Fig. 11B). A small subtriangular cell with polar flagellum (b2 in Fig. 9B) may also belong to the same group.

MICROBORINGS

In the Upper Tithonian Crassicollaria Zone, calcareous dinoflagellate cysts occur as nuclei of some micro-oncoids (Fig. 8A, B). Traces of boring can be seen in the wall, as well as in the calcite infilling the central area of the calcareous dinocyst (bg in Fig. 8B). The diameter of the microborings is 0.2–0.5 µm. Some uniseriate microbial filaments are present in these microborings (f in Fig. 8B); their width is 0.3–0.5 µm and length attains ~10 µm. The traces of activity of microbial endoliths also occur in other microfossils, such as *Globochaete alpina* Lombard (Chitinoidella Zone, Tithonian) embedded in some micro-oncoids (Fig. 12A). The microborings are 0.6–2.8 µm in diameter (bg in Fig. 12B). Therefore, encrusting of *G. alpina* by microbial filaments was preceded by activity of microbial endoliths. Similar microborings were also observed in the walls of some calcareous dinocysts that are not coated by microbial filaments.

DISCUSSION AND INTERPRETATION

MICROBIAL FILAMENTS

1. **Thin uniseriate filaments**. According to Leinfelder (1985), exact taxonomic differentiation of fossil cyanobacterial structures is impossible in rocks older than the Pleistocene. A more detailed comparison of the Upper Jurassic microbial filaments with the modern taxa of bacteria (cyanobacteria) is difficult or impossible, because definitions of the genera are based on a combination of molecular, morphological and ecological criteria (Komárek et al., 2014). Therefore, in this study comparisons and interpretations of the Upper Jurassic microbial morphotypes with some fossil and modern bacteria are based on analysis of only their morphological features and dimensions.

Although the shape of the microbial filaments from the RTL Fm. may sometimes resemble tubes of *Girvanella* Nicholson and Etheridge (Wood, 1957; Riding, 2006; Bucur et al., 2014) or "*Rivulariacean*-type cyanobacteria" (Uţa and Bucur, 2003), their dimensions and structure details are quite different. The *Girvanella* and "*Rivulariacean*-type cyanobacteria" fossil filaments are >3 µm in diameter (between 3 and 30 µm and larger). The *Girvanella* filaments from the Kimmeridgian of Crimea were shown to be 5 to 9 µm wide (Bucur et al., 2014: fig. 15k), but those from the Upper Jurassic of Poland seem to be even thinner (~3 to 8 µm in diameter – Matyszkiewicz et al., 2006: fig. 5F). Other fossil filaments named "*Rothpletzella/Pseudorothpletzella*-like structures" (Bucur et al., 2014: fig. 16h–j) are also 3.5–5 µm wide; moreover, their short tubes terminated with globular cells are not similar to the microbial filaments from the Upper Jurassic limestones of the Mały Giewont area. The filaments of the modern cyanobacteria *Plectonema gloeophilum* Borzi – now *Leptolyngbya gleophilum* (Borzi) Anagnostidis and Komárek – considered the equivalent of the fossil *Girvanella* are ~4.5 to 7 µm in diameter (Riding, 1977: pl. 11). The Recent *Leptolyngbya* sp. from the intertidal zone of the Portuguese coast has filaments 1.7–5 µm wide (Brito et al., 2012: fig. 2n). The modern representatives of the genus *Rivularia* Agardh ex Bonet and Flahault have tapering filaments 2–25 µm wide (Ulcay et al., 2014). The simple microbial filaments from the Jurassic Mn crust (Northern Morocco – Reolid et al., 2011: fig. 10) are also thicker (~1–3 µm in diameter) than the uniseriate filaments in the studied RTL Fm. limestones (0.2–1 µm).

The microbial bundles from the RTL Fm. are much smaller than the "paintbrush-like micritic tufts" from the Jurassic Portugal oncoids (*Dichothrix* morphotype – Leinfelder, 1985: 260 and pl. 30/7). These "micro-colonies" of microbial filaments from the RTL Fm. limestones are roughly similar to the bundles of bacteria, 1–3 µm in width, illustrated from the Middle Eocene of Egypt ("mineralized leptothrix-like bacterial bundles" – Salama et al., 2013: fig. 9C, D). Nevertheless, the Eocene bacterial bundles are more compact than those occurring in the studied Upper Jurassic limestones (for example, f1 in Fig. 10C). In contrast, the modern species *Leptothrix lopholea* Dorff (phylum Proteobacteria – Garrity and Holt, 2001) forms aggregates, ~30–45 µm in diameter, composed of many trichomes radiating from a cluster of holdfasts (van Veen et al., 1978; Spring, 2006). Moreover, the trichomes of *L. lopholea* (and of the *Sphaerotilus–Leptothrix* group in general) are not terminated with larger apical cells, as in the case of the studied microbial fil-

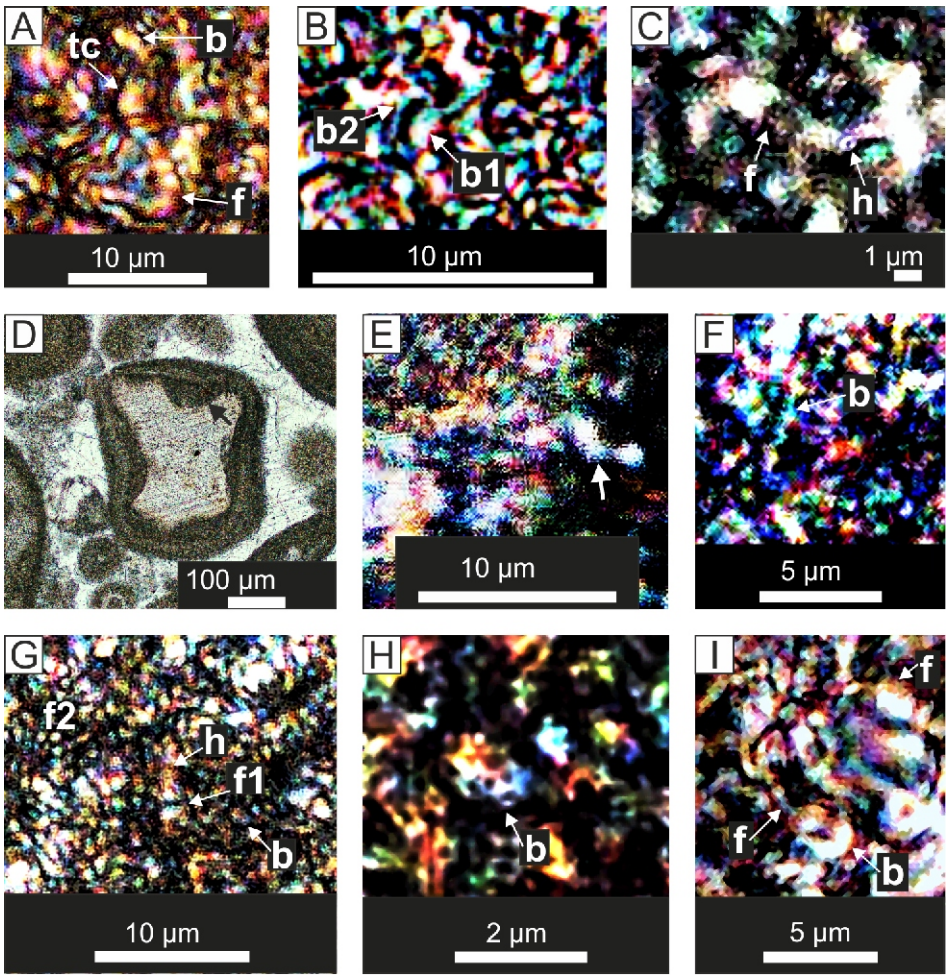
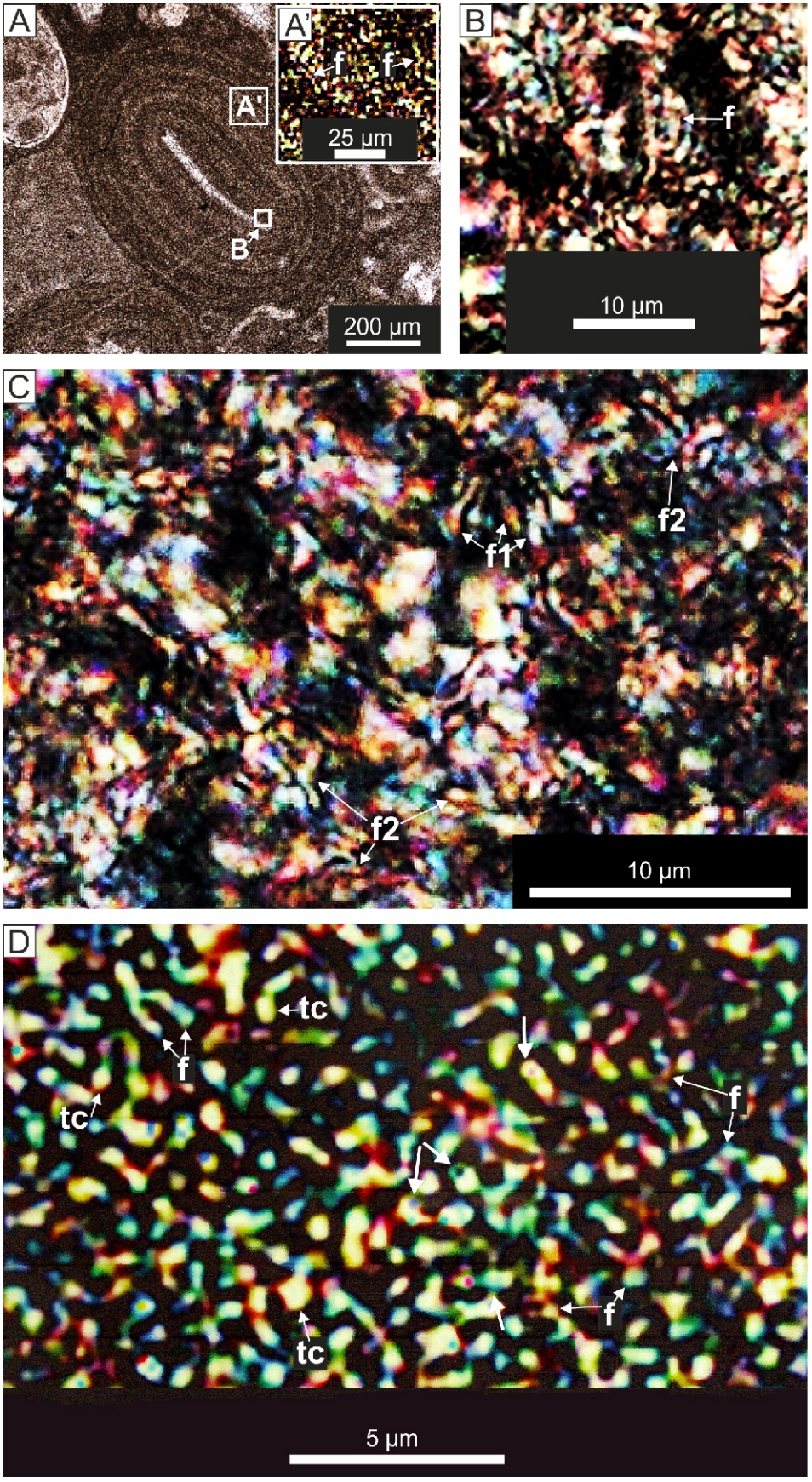


Fig. 9. Upper Kimmeridgian and Tithonian bacteria

A – microbial filament, 10 1.6 µm (f), terminated with a larger cone-shaped cell (tc) and a bacterium (3.0 1.2 µm) with a tuft of short polar flagella (b), peloid (sample/thin-section G-27, section B in Fig. 2, Moluccana Zone, Upper Kimmeridgian); **B** – bacteria in a peloid, 355 304 µm: (b1) monotrichous bacterium, 1.5 0.8 µm, supported with a spiral flagellum, 2 µm long, (b2) small monotrichous body, 0.8 0.5 µm, with a flagellum, 1 µm long (sample/thin-section G-32, section B in Fig. 2, Moluccana Zone, Upper Kimmeridgian), crossed polars; **C** – tapering filament, 5.5 0.8–1.5 µm (f), in a micro-oncoid, (h) button-like cell (holdfast?, sample/thin-section G-67, section B in Fig. 2, Chitinoidella Zone, Tithonian); **D** – micro-oncoid formed around an echinoderm bioclast, arrow indicates location of the filament shown in Figure 9E (sample/thin-section G-69, section B in Fig. 2, Chitinoidella Zone, Tithonian); **E** – enlarged fragment of the micro-oncoid shown in Figure 9D, arrow indicates a spiral microbial filament (Cyanobacteria), ~13 1.8 µm (crossed polars); **F** – fragment of a Lower Kimmeridgian micro-oncoid with a spiral bacterium (b), 5.1 0.3-0.6 µm (sample/thin-section MG-69, section A in Fig. 2); **G** – fragment of a micro-oncoid from the Malmica Zone (Lower Tithonian): (b) monotrichous bacterium, (f1) tapering filament, 4.5 2 µm, with a button-like cell (h – holdfast?), (f2) thin filaments forming dense microbial thicket (sample/thin-section G-55, section B in Fig. 2); **H** – enlarged monotrichous bacterium (b) from Figure 9G (1.5 1.0 µm, flagellum ~1.5 µm long, sample/thin-section MG-107, Chitinoidella Zone, Tithonian); **I** – small fragment of a micro-oncoid from the Chitinoidella Zone, Tithonian: (b) monotrichous(?) bacterium, 2.2 1.0 µm, (f) branched filaments (sample/thin-section MG-107, section A in Fig. 2)


A
A'
f
f
25 µm
A'
B
200 µm
B
f
10 µm
C
f2
f1
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tc
5 µm

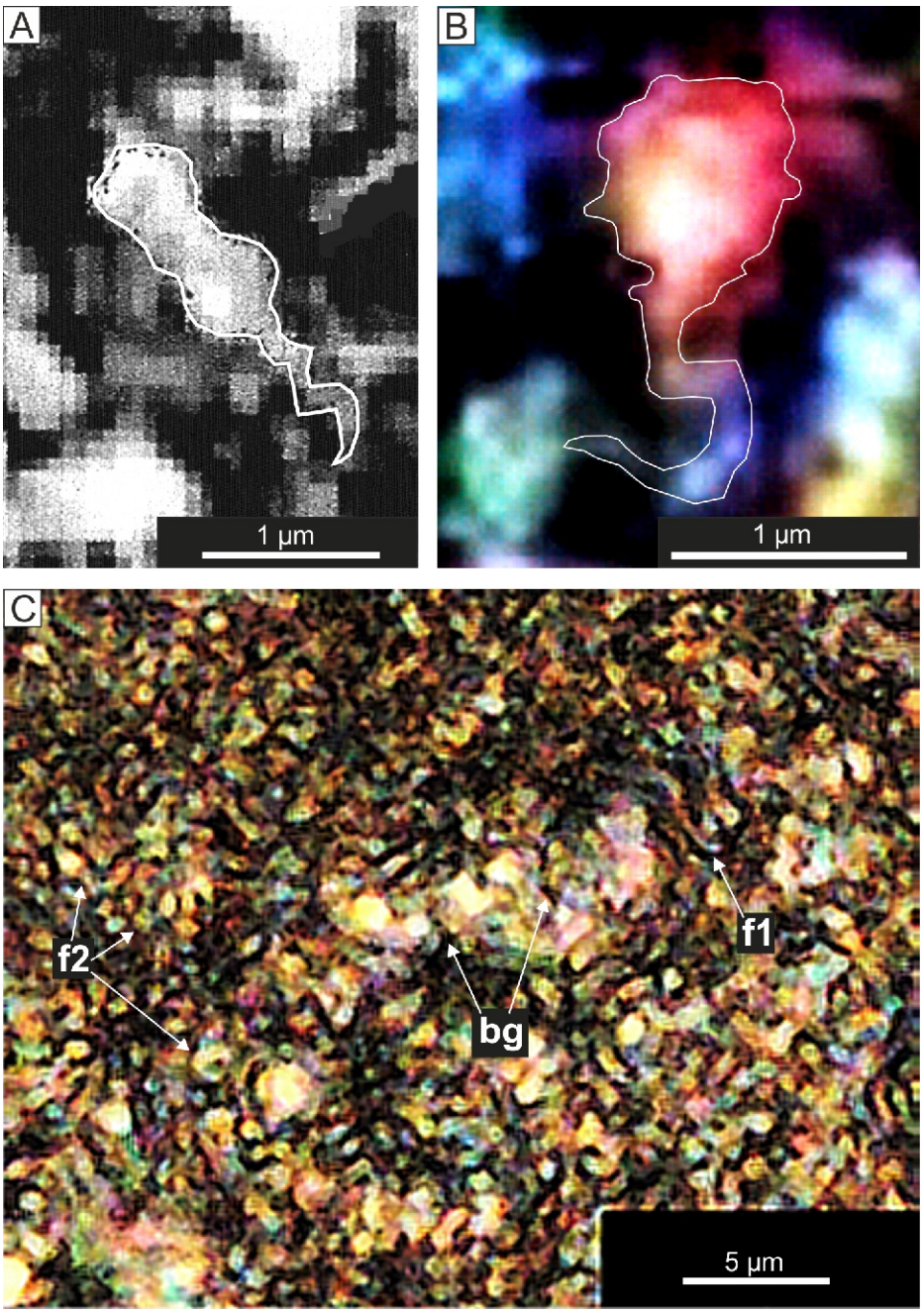

Fig. 11A – enlarged LM photomicrograph of the bacterium from Figure 3C (b), the contour of the bacterium is drawn as a white line (sample/thin-section G-40, section B in Fig. 2, uppermost Kimmeridgian); B – enlarged LM photomicrograph of a small coccoid body with a polar flagellum (= b3 in Fig. 7C), the contour of this microbial form is shown as a white line (sample/thin-section G-69, section B in Fig. 2, Chitinoidella Zone, Tithonian); C – contact of a fragment of microbial mat (darker upper part of the LM photomicrograph) with the surrounding biointraclastic deposit in the lower part of the image: (f1) dark uniseriate microbial filament (6 0.75 µm) clearly different from (f2) the thinner filaments forming the dense meshwork shown in the upper part of the photograph, (bg) microborings, ~0.4 µm wide, in an intraclast (sample/thin-section G-27, section B in Fig. 2, Mollucana Zone, Upper Kimmeridgian), crossed polars

Fig. 10. Microbial filaments from Tithonian micro-oncoids and a peloid

A – micro-oncoid (895 618 µm) from the Crassicollaria Zone (Upper Tithonian, sample/thin-section MG-107, section A in Fig. 2); white rectangles: A' indicates the area enlarged in the inset A' (f – large spiral microbial filaments), and B shows the location of Figure 10B; **B** – enlarged fragment of the micro-oncoid shown in Figure 10A: (f) microbial filament, 14 µm long, with an ovoid cell and lateral offshoot (crossed polars); **C** – enlarged fragment of another micro-oncoid (780 µm in diameter, also from thin-section MG-107): (f1) uniserial microbial filaments (3.5 0.3–0.5 µm) forming a basket-like bundle in a reversed position, 6 µm in diameter, (f2) branched filaments; **D** – microbial filaments in an elongate peloid (faecal pellet?): (f) true branched filaments, (tc) larger terminal cells, thick arrows indicate transversal cross-sections of the filaments – a central "empty" canal can be discerned (sample/thin-section G-68, section B in Fig. 2, Chitinoidella Zone, Tithonian), crossed polars

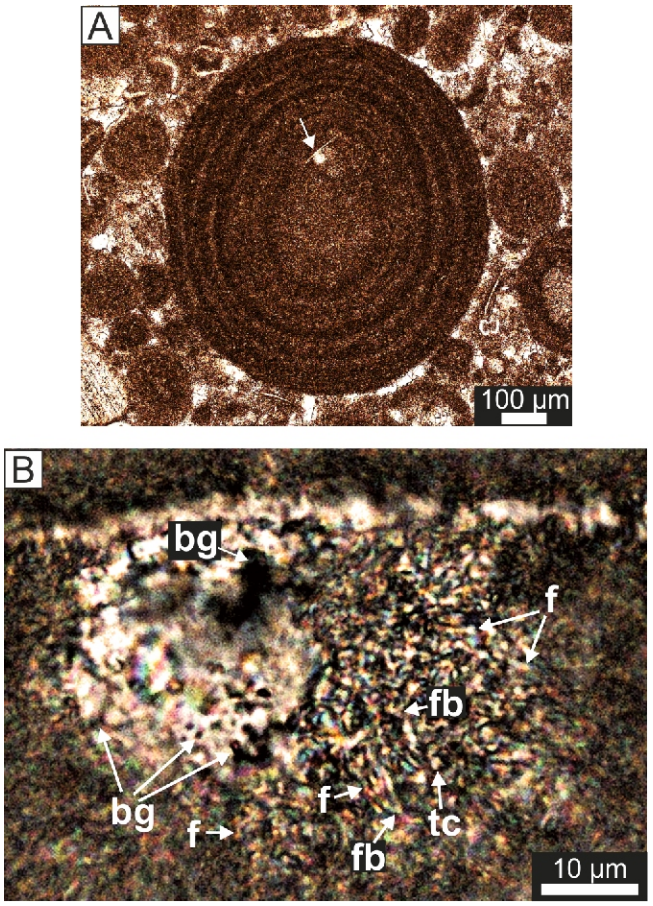

Fig. 12A – micro-oncoid from a Tithonian limestone (Chitinoidella Zone): arrow indicates *Globochaete alpina* in the marginal part of the peloidal nucleus (sample/thin-section MG-105, section A in Fig. 2); B – higher magnification of the *Globochaete alpina* from Figure 12A (rotated 45° clockwise with respect to Fig. 12A): (f) straight tube-like microbial filaments, 0.5–0.7 µm in diameter, sharply terminated or having a larger apical cell (tc), some are cup-shaped, the filaments reach a length of ~10 µm, some branched (T-shaped) filaments are also present (fb), the bioclast of *Globochaete alpina* is pierced by microborings (bg), 0.6–2.8 µm wide (sample/thin-section MG-105, section A in Fig. 2, Chitinoidella Zone, Tithonian), crossed polars

aments from the RTL Fm. Some other modern bacteria, such as *Thiotrix* spp. (phylum Proteobacteria – Garrity and Holt, 2001), form rosettes, ~15–30 µm in diameter (Unz and Head, 2005). However, *Thiotrix* spp. rosettes are clearly different from the fossil microbial bundles found in the RTL Fm. of the Mały Giewont area, and the filaments of the compared bacteria are dissimilar.

In many modern filamentous cyanobacteria, nitrogen fixation occurs in differentiated cells called heterocytes or heterocysts (Thiel et al., 1995; Vincent, 2009; Kumar et al., 2010). Usually, these cells are of larger size and have a thicker wall than the vegetative cells (Tyagi, 1975). If no source of combined nitrogen is available, heterocytes develop in semiregular intervals along a filament of vegetative cells (Maldener and Muro-Pastor, 2010). The cone-shaped or ovoid terminal cells of uniseriate filaments from the studied limestones (RTL Fm.) are similar to heterocytes of some recent cyanobacteria. According to Rippka et al. (1979) and Adams and Duggan (1999), heterocysts (= heterocytes) are formed by filamentous cyanobacteria of subsections IV and V (orders Nostocales and Stigonematales, respectively, after Komárek et al., 2014). The uniseriate microbial filaments terminated with spindle-form cells are characteristic for some representatives of the modern genera *Nostoc* Vaucher, *Cylindrospermopsis* Seenayya and Subba-Raju and *Cylindrospermum* Kützing (Rippka et al., 1979, 2001a).

In general, the modern cyanobacteria vary in diameter from <1 to >100 µm (Adams and Duggan, 1999). The trichomes of cyanobacteria from the above-mentioned genera are usually much thicker than the fossil filaments occurring in the studied Upper Jurassic limestones from the Western Tatra Mountains. Only the representatives of the genus *Cylindrospermopsis* possess thin trichomes (<4 µm in diameter according to Rippka et al., 2001a). Indeed, the illustrated filaments of *Cylindrospermopsis* (Rippka et al., 2001a: fig. B10.75) are ~0.8 µm in diameter. The presence of the heterocyte-like terminal cells is the characteristic feature of the studied thin microbial filaments, suggesting their interpretation as cyanobacteria similar to the modern order Nostocales and – perhaps – to the family Nostocaceae C.A. Agardh ex Kirchner (Komárek et al., 2014). The uniseriate filaments from the Upper Jurassic limestones of the Mały Giewont area probably belonged to the fossil group of cyanobacteria characterized by relatively short and extremely thin trichomes (see, for example, f in Fig. 7C). These filaments form a dense meshwork or oval bundles within the micro-oncoids (Figs. 7B and 9G), peloids (Figs. 3B, C, 6B and 7D), and fragments of microbial mats, and sometimes in the deposit between these allochems (Fig. 4F). The tube-like form (filament) shown in Figure 5E indicates that in this case calcification was external to the cells and occurred in the extracellular sheath (cf. Riding, 1991, 2011). The specific feature of the figured tube-like form is a fine-grained (amorphous?) structure of $CaCO_3$ present in the calcified microbial sheath.

2. **Large multi-cell filaments**. The microbial filament shown in Figure 9A belongs to heterocytous cyanobacteria (section IV after Rippka et al., 1979; order Nostocales according to Komárek et al., 2014). The shape of the discussed filament resembles, in general, the modern genus *Nostoc* Vaucher (cf. Rippka et al., 1979). This group of microbial filaments seems to be uncommon in the studied Upper Jurassic limestones in the Mały Giewont sections.

3. **Large spiral filaments**. The relatively large spiral microbial filament (Fig. 9E) from the Tithonian micro-oncoid belongs to cyanobacteria. Similar spiral microbial filaments are also present in the Late Tithonian micro-oncoid illustrated in Figure 10A (with inset A'). The Kimmeridgian filaments reported from Germany (see Briggs et al., 2005: fig. 4b) display a different (ribbon-like) spiral structure. The Tithonian filament (Fig. 9E) is similar to some modern representatives of the order Spirulinales (Komárek et al., 2014), and possibly also to Synechococcales, e.g. *Leptolyngbya lagerheimii* (Gomont) Anagnostidis and Komárek (cf. Martins et al., 2012: fig. 5). In contrast, the spiral trichomes of the genus *Arthrospira* Stizenberger from the order Oscillatoriales (Komárek et al., 2014) are 3–16 µm wide (Li et al., 2001; Dadheech et al., 2010).

4. **Tapering filaments**. The shape of tapering microbial filament shown in Figure 4D is similar to the young trichome of *Calothrix* (Rippka et al., 1979: fig. 61). However, some marine strains of *Calothrix* have been transferred to the genus *Rivularia* (Rippka et al., 2001b). Therefore, the above-indicated filament may be compared, in general, with the modern family *Rivulariaceae* Kützing ex Bornet et Flahault. In contrast, the filaments labelled f in Figure 9C and f1 in Figure 9G are similar to baeocytes of some modern *Pleurocapsa*-group strains (Waterbury and Stanier, 1978; Rippka et al., 2001c). These fossil filaments have a button-like cells at their narrower end (h in Fig. 9C, G), which resemble the holdfast at the distal end of the

stalk in some modern representatives of the *Caulobacter* group of Proteobacteria (Poindexter, 1964: fig. 12c).

5. **Branched filaments**

(a) The microbial filament labelled f1 in Figure 5C, D, with minor lateral branches and a terminal cup-shaped cell, is 1.0–1.4 μm in diameter. It probably belongs to Nostocales (Komrek et al., 2014), although is very thin in comparison with recent branched representatives of this group.

(b) The heteropolar filament with branches (Fig. 7G), located in the marginal part of a peloid from the Tithonian Chitinoidella Zone (Fig. 7E), resembles some modern cyanobacteria grouped in section V (Rippka et al., 1979), later placed in the order Nostocales (Komárek et al., 2014). The subglobular cell at one end of the filament (tc in Fig. 7G) is similar to terminal heterocytes of the modern genera *Cylindrospermum* and *Nostoc* (cf. Rippka et al., 1979: figs. 36 and 39) from the family Nostocaceae (Komárek et al., 2014). The other end of the filament resembles rather that of larger (modern) cyanobacteria from the genus *Scytonema* Agardh (Fowler, 2011: fig. 48a; Komárek et al., 2013: fig. 6c), which belongs to the family Scytonemataceae Rabenhorst ex Bornet et Flahault (Komárek et al., 2014). However, the presence of lateral (true) branches is characteristic for the family Stigonemataceae, also from the order Nostocales. The modern genus *Stigonema* is polymorphic and consists of several morphotypes (also heteropolar – Komárek et al., 2014).

(c) Branched microbial filaments occur also in the micro-oncoids from the Upper Tithonian limestone (f in Fig. 9I and 10A, B, f2 in Fig. 10C). A filament with an offshoot growing out from the oval-shaped cell (f in Fig. 10B) resembles some modern true-branched Nostocales (Komárek et al., 2014).

(d) Other branched microbial filaments occur in the Tithonian peloid (faecal pellet? – Fig. 10D). Larger terminal cells of some filaments (tc in Fig. 10D) suggest the presence of cyanobacterial heterocytes. However, the filaments are very thin in comparison with the modern true-branched cyanobacteria (cf. Rippka et al., 1979) assigned to Nostocales (Komárek et al., 2014). Reolid and Abad (2014) described "Jurassic microbial filaments preserved as glauconite with cylindrical shape with an empty central canal." However, their filaments (illustrated in figs. 4, 6 and 7 of the cited paper) are clearly much larger (for example, "green filaments grow perpendicular to the lamination, measuring 100–450 μm in length" – page 392; the filaments are about 20 to 30 μm wide in fig. 6b) and therefore cannot be compared with the thin filaments shown in my Figure 10D.

NON-FILAMENTOUS BACTERIA (MAINLY PROTEOBACTERIA)

This group comprises the following fossil bacteria: rod-shaped (bacilli), vibrios, spirilla and their coccoid bodies.

1. The rod shape and length of the fossil specimen shown in Figure 3B (streptobacillus? – uppermost Kimmeridgian) are similar to those of some modern marine bacteria from the family Halomonadaceae (the order Oceanospirillales of Proteobacteria – Garrity and Holt, 2001), e.g. *Halomonas* Vreeland, Litchfield, Martin, and Elliot, emend. Dobson and Franzmann (Vreeland, 2005). However, the fossil bacterium is thinner than representatives of the *Halomonas* species. Some modern analogues may also be found among bacteria from the phylum Firmicutes (Garrity and Holt, 2001), especially in the family Bacillaceae (Nielsen et al., 1995; Logan and De Vos, 2009; Bahamdain et al., 2015). Although the bacillus-shaped bacteria illustrated from the Jurassic of the Betic-Rifian Cordillera (Reolid, 2011: fig. 11C, D) differ from the specimen shown in Figure 3B, perhaps some modern marine representatives of the genus *Bacillus* Cohn comprise forms roughly similar to the discussed Kimmeridgian bacterium.

2. (a) The fossil specimen illustrated in Figures 3C (b) and 11A is similar to modern monotrichous bacteria (cf. Kayser, 2007: fig. 3.1: 12), in particular to some representatives of the genera *Vibrio* Pacini (Farmer III et al., 2005: fig. BXII. .158) and *Bdellovibrio* Stolp and Starr (Nuñez et al., 2003; Jurkevitch, 2006). Modern monotrichous rod-shaped bacteria are represented also in the genera: *Salinivibrio* Mellado, Moore, Nieto and Ventosa (Ventosa, 2005), *Pseudomonas* Migula (Lighthill, 1976; Baumann et al., 1983; Palleroni, 2005) and *Shewanella* MacDonell and Colwell (Bowman, 2005; Roh et al., 2006).

(b) Another monotrichous bacterium from the same peloid (uppermost Kimmeridgian) is composed of a rod-shaped cell with one polar flagellum ~1.7 μm in length (Fig. 4B). Similar bacteria occur also in the Tithonian oncosparite (b1 in Fig. 7C). Three monotrichous bacteria indicated as b in Figure 4F seem to penetrate from outside the marginal zone of the peloid composed mainly of thin uniseriate microbial filaments (f). Such location of these fossil bacteria suggests their heterotrophic character.

3. The shape of the bacterium shown as b in Figure 9G, H is roughly similar to the modern species *Marinomonas mediterranea* Solano and Sanchez-Amat 1999, 1245^{VP} (Sanchez-Amat and Solano, 2005: fig. BXII. .106) from the family Oceanospirillaceae (phylum Proteobacteria – Garrity and Holt, 2001).

4. A bacterium with many short tubular appendages (b in Fig. 6B) occurs in the marginal zone of the peloid (Fig. 6A) from the Upper Kimmeridgian limestone. Some modern marine vibrios have tubular appendages (Farmer III et al., 2005: fig. BXII. .174) roughly similar to those of the Kimmeridgian bacterium.

5. A comma-shaped lophotrichous vibrio (b in Fig. 9A) differs from the above-mentioned rod-shaped bacteria mainly by a polar tuft of short flagella. This is difficult, however, to indicate a similar modern taxon among the marine Vibrionaceae.

6. A crescent-shaped bacterium with a single spiral flagellum (b1 in Fig. 9B) is similar to some modern bacteria from the genus *Caulobacter* (Poindexter, 1964, 1989; Jannasch and Jones, 2003), which belongs to the phylum Proteobacteria (Garrity and Holt, 2001). The marine representatives of the genus *Hydrogenovibrio* Nishihara, Igarashi and Kodama are roughly similar in shape and have a single polar flagellum (the species *H. marinus* – Nishihara, 2005). In addition, some representatives of the modern genus *Beneckea* Campbell (Baumann et al., 1971) from Vibrionaceae are similar to the discussed bacterium found in the Upper Kimmeridgian limestone.

7. In comparison with the spiral microbial filaments (spirilla) from the studied Upper Jurassic limestones (b in Fig. 4A, b2 in Fig. 7C, s in Fig. 7F), some modern Bacteroidetes from the family Spirosomaceae (Larkin and Borrall, 1978, 1984), for example *Larkinella* (Kulichevskaya et al., 2009), display a similar – albeit not identical – shape. Cells of the modern helical-shaped bacteria from the Pacific Ocean, assigned to *Salinispira pacifica* gen. nov., sp. nov. (Ben Hania et al., 2015), and from the species *Spirochaeta isovalerica* sp. nov. (Harwood and Canale-Parola, 1983) are similar in diameter. Both taxa are assigned to the phylum Spirochaetes. However, the helical coiling of those taxa (a wavelength of 1.0 μm and an amplitude of 0.6 μm for *S. isovalerica* according to Harwood and Canale-Parola, 1983) is less tight in comparison with the fossil specimens from the Western Tatra Mountains shown in Figure 4A (a wavelength of 0.4 μm and an amplitude of 0.3–0.4 μm). The dimensions of the fossil bacterium illustrated in Figure 7F are close to those of the modern species *Spirillum volutans* (Krieg), but the bipolar flagellar fascicles typical of this taxon (Krieg, 2006) are not visible in the Upper Jurassic specimen. Moreover, *S. volutans* occurs in stagnant freshwater envi-

ronments (Krieg, 2006). Modern (marine) Oceanospirillaceae are motile by polar flagella as well (Garrity et al., 2005; Pot and Gillis, 2005). The shape of the larger spirillum (b in Fig. 9F) is roughly similar to that of phosphatized spiral microbes from the Kimmeridgian of Germany (Briggs et al., 2005), which are much longer and better preserved.

8. The subglobular to subtriangular cells with spiral flagellum (b3 in Fig. 7C and 11B, b in Fig. 7D and b2 in Fig. 9B) are similar to coccoid bodies, or microcysts, produced by some modern spirilla (Williams and Rittenberg, 1956; Krieg, 1976: fig. 20F; Satomi et al., 1998).

MICROBORINGS OF ENDOLITHIC BACTERIA

Among the fossil ichnotaxa (microendoliths) similar to modern cyanobacteria, *Scolecia filosa* Radtke (Glaub et al., 1999) resembles the miroborings observed in the Upper Jurassic micro-oncoids of the RTL Fm. The ichnotaxon *S. filosa* is known to be of wide palaeobathymetric range. The cyanobacterium *Leptolyngbya terebrans* (Bornet and Flahault ex Gomont) Anagnostidis and Komárek is considered to be the modern executor of *S. filosa* microborings (Glaub et al., 1999; Carreiro-Silva et al., 2009, 2012). Trichomes of *L. terebrans* are 0.95–1.5 μm wide (Gomont, 1893; Ghirardelli, 2002, 2003). The Upper Kimmeridgian uniseriate non-heterocytous filament (shown as f1 in Fig. 11C) resembles *L. terebrans*. The species *Plectonema terebrans* (now *L. terebrans*) is known to be the "low-light specialist" with a broad bathymetrical range of occurrence (Le Campion-Alsumard, 1979; Chazottes et al., 2009). According to Le Campion-Alsumard (1979), *Plectonema terebrans* occurs to a depth of 80 m in the region of Marseilles, but was also found in deeper waters (370 m – Golubic et al., 1999; Glaub, 2004). Gektidis et al. (2007) have dismissed *Scolecia filosa* as a potential key ichnotaxon because of the broad bathymetrical range of the modern taxon *L. terebrans*.

The thinnest microborings (0.2–0.5 μm in diameter) found in the Upper Jurassic limestones of the RTL Fm. perhaps resemble another group of (modern) ichnofossils named "Pygmy form", probably of bacterial origin (Glaub, 2004; Radtke et al., 2011). The Upper Tithonian microbial filaments (0.3–0.5 μm in diameter), terminated with cone-shaped or oval elongate cells, occur in some microborings (f in Fig. 8B).

ALLOCHTHONOUS *VERSUS* AUTOCHTHONOUS ORIGIN OF MICRO-ONCOIDS AND PELOIDS

The interpretation of the pelagic "oolites" as micro-oncoids that "grew, at least partially, by particle accretion" (Jenkyns, 1972) is not confirmed by the present study. The Upper Kimmeridgian–Tithonian micro-oncoids from the RTL Fm. were formed mainly by thin filamentous bacteria (cyanobacteria) that overgrew successively their nuclei with a few to several laminae. The trapped (accreted) bioclasts (microfossils, nannofossils), although present in the cortices of micro-oncoids, are not volumetrically important components. This explanation confirms interpretation suggested – albeit not documented with high-magnification photomicrographs – by Lefeld and Radwański (1960). Therefore, the studied micro-oncoids (*sensu* Kutek and Radwański, 1965) can also be named "cyanoids" (Flügel, 2004: fig. 4.14) or "microcyanoids". The peloids occurring in the Upper Kimmeridgian–Tithonian limestones are packed with the filamentous bacteria (cyanobacteria) indicating roughly similar environmental conditions of their origin with respect to micro-oncoids.

According to Lefeld and Radwański (1960: 603), the ooids (or "pseudo-ooids") are mainly allochthonous and were transported "from the shallower zones by weak bottom currents". This inference is probably true as concerns the limestones displaying a subtle bedding (Lefeld and Radwański, 1960) and those beds that contain ooids with preserved radial structure (this study, Fig. 5B). However, some peloids and micro-oncoids occur in the biomicrites containing similar microbial filaments inside and outside these grains (Figs. 3C, 4F and 10A). Their allochthonous provenance is not evident; therefore, autochthonous origin is also probable. Moreover, frequent occurrence of pelagic microfossils as nuclei of micro-oncoids (Lefeld and Radwański, 1960; Mišik, 1998; Pszczółkowski et al., 2016) does not match with a transport of these coated grains from much shallower sedimentary environments. The thin uniseriate fossil filaments filling up the peloids and micro-oncoids could be adapted to conditions that existed in the sublittoral zone ("tens of metres" – Jenkyns, 1972) below the wave base (Lefeld and Radwański, 1960; Pszczółkowski et al., 2016).

CONCLUSIONS

1. Two informal groups of fossil bacteria have been found in the Upper Jurassic carbonates of the Raptawicka Turnia Limestone Formation in the Mały Giewont sections of the Western Tatra Mountains (Poland): (A) microbial filaments and (B) non-filamentous bacteria. The first group is further subdivided into (1) thin uniseriate filaments, (2) large multi-cell filaments, (3) large spiral filaments, (4) tapering filaments and (5) branched filaments.

2. The thin uniseriate filaments are the main microbial component of the peloids and micro-oncoids occurring in the studied RTL Fm., mainly in the Upper Kimmeridgian–Tithonian. The presence of the heterocyte-like terminal cells suggests their interpretation as cyanobacteria similar to the modern order Nostocales and perhaps to the family Nostocaceae. These filaments belong probably to the fossil group of cyanobacteria characterized by rather short and extremely thin trichomes.

3. The large multi-cell filaments are uncommon in the studied limestones. These uniseriate filaments are interpreted as cyanobacteria similar to modern taxa also belonging to the order Nostocales. The large spiral filament from the Tithonian micro-oncoid is similar to some modern Spirulinales and possibly also to Synechococcales.

4. The tapering filaments are uncommon in the studied thin-sections. One of those filaments resembles some representatives of the modern family *Rivulariaceae*, whereas other specimens are similar to baeocytes of some modern *Pleurocapsa*-group strains.

5. The Tithonian heteropolar filament with minor branches (from the Chitinoidella Zone) resembles some modern cyanobacteria from the order Nostocales. Other branched microbial filaments found in the Tithonian limestones, although thinner, are probably also comparable with some modern representatives of the order Nostocales.

6. Fossil non-filamentous bacteria found in the studied Kimmeridgian–Tithonian limestones comprise rod-shaped bacilli, monotrichous bacilli and spirilla. These bacteria belong mainly to the phylum Proteobacteria. A few tiny subglobular microbes from the Tithonian micro-oncoid are similar to coccoid bodies produced by some modern spirilla.

7. Some microborings observed in the microfossils occurring in the micro-oncoids of the RTL Fm. resemble the ichnotaxon *Scolecia filosa* Radtke known to be of wide palaeobathymetric range. The thinnest microborings resemble another group of ichnofossils named "Pygmy form", probably also of bacterial origin.

8. The Upper Kimmeridgian–Tithonian micro-oncoids from the RTL Fm. were formed mainly by filamentous bacteria (cyanobacteria) that overgrew successively their nuclei with a few to several laminae. This explanation confirms interpretation suggested earlier by Lefeld and Radwański (1960).

9. Frequent occurrence of pelagic microfossils in the micro-oncoids does not match with a transport of these coated grains from much shallower sedimentary environments. The fossil filamentous bacteria filling up the peloids and micro-oncoids could be adapted to conditions that existed in the sublittoral zone below the wave base.

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