Lower Oligocene non-geniculate coralline red algal (Corallinales, Rhodophyta) assemblage from Poljšica pri Podnartu (Upper Carniola, Slovenia)

Spodnjeoligocenska združba nečlenjenih koralinej (Corallinales, Rhodophyta) iz Poljšice pri Podnartu

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Abstract

The Lower Oligocene Gornji Grad beds from Poljšica pri Podnartu consist of marly limestone, mudstone, several layers of limestones and two layers of sandstones, and were deposited on a mixed carbonate-siliciclastic ramp. Especially the limestones contain rich fossil fauna and non-geniculate coralline red algae. These were systematically collected from four horizons and researched in thin sections under an optical microscope. Genera *Lithoporella*, *Neogoniolithon*, *Spongites*, *Lithothamnion*, *Mesophyllum* and *Spongites* were recognized. Surface area for each genus was calculated and the differences in the coralline assemblages in the four horizons were analysed. The corallines originate from two source areas: sandy-muddy bottom of a shallow marine environment, and small coral bioherms with its encrusters.

Izvleček

Gornjegrajske plasti pri Poljšici pri Podnartu so se odlagale tekom spodnjega oligocena na karbonatnosiliciklastični rampi. Sestavlja jih zaporedje laporastega apnenca, muljevca, apnenca in peščenjaka. Posebno plasti apnenca so izredno bogate s fosili, med katerimi so tudi nečlenjene rdeče alge reda Corallinales (koralineje). Te so bile sistematično vzorčevane v štirih horizontih. S pomočjo optičnega mikroskopa je bilo določenih šest rodov: *Lithoporella, Neogoniolithon, Spongites, Lithothamnion, Mesophyllum* in *Spongites.* Razmerje med posameznimi rodovi se v profilu spreminja. Prepoznani sta bili dve izvorni območji koralinej: peščeno-muljasto plitvo morsko dno in manjše koralne bioherme, kjer koralineje nastopajo kot epifitski organizmi.

Introduction

The westernmost outcrops of the Lower Oligocene Gornji Grad beds (informal lithostratigraphic unit) in Slovenia can be found near Bohinj (HERLEC, 1985), from where minor bodies of limited size extend further to the east (GRAD & FERJANČIČ, 1976; MIOČ, 1978, 1983; BUSER, 1979; PREMRU, 1983; BUSER, 1986; JURKOVŠEK, 1987). Especially known for its rich fossil content are beds at Poljšica pri Podnartu (Upper Carniola) and in the Gornji Grad area (Styria). Deposition of the Gornji Grad beds corresponds to a gradual tectonic subsidence of the area, as well as to a long term eustatic sea-level rise (RÖGL, 1998; JELEN et al., 1998; NEBELSICK et al., 2000; SCHMIEDL et al., 2002).

HEMLEBEN (1964) divided Oligocene beds in the Gornji Grad area into four units:

Basal unit (1) consists of conglomerates, mudstones and sandstones, deposited in the braided river (BRUCH, 1998) or in the deltaic environment (SCHMIEDL et al., 2002). Scherbacher (NEBELSICK et al., 2000) determined Late Eocene to Early Oligocene age of these strata. The thickness of the Basal unit is between few to 400 m (HEMLEBEN, 1964; NEBELSICK et al., 2000). They discordantly overlie rocks of Triassic age (HEMLEBEN, 1964).

Upon Basal unit or directly upon Eocene or Triassic basement transgressively lie the Gornji Grad beds (2), a variable stack of marly and sandy limestones, limestones, marlstones and mudstones. The whole succession is 5-30 m thick (HEMLEBEN, 1964). DROBNE et al. (1985) have proven basal Oligocene age of these beds. Detailed microfacies analysis and palaeoenvironmental researches for these beds have recently been made for the Gornji Grad area by NEBELSICK et al. (2000), SCHMIEDL et al. (2002) and NEBELSICK et al. (2005). BASSI and NEBELSICK (2000) and BASSI et al. (2000) have described several genera and species of red and green algae. BLED



Hundar. Austria **KRANJ** Italy Slovenia 10 km Croatia

Fig. 1. Location of investigated area. Asterisk marks the position of Poljšica pri Podnartu.

Sl. 1. Položaj obravnavanega ozemlja. Lega Poljšice pri Podnartu je označena z zvezdico.

The Gornji Grad beds are followed by a 170-270 m (HEMLEBEN, 1964) thick unit of marine clay (Tegel unit) (3) of the Oligocene age (CIMER-MAN, 1967; PAVŠIČ, 1983, 1985; Herlec, 1985; BRICL & PAVŠIČ, 1991). Transition between the Gornji Grad beds and the Tegel unit is gradual or sudden (NEBELSICK et al., 2000).

Finally, 800-1000 m thick sequence, consisting of silty marls and tuffites of the Late Oligocene to Early Miocene age of the vulcanoclastic Tuffite unit (4) follows (NEBELSICK et al., 2000).

The succession of just described units, with the exception of the Tuffite unit, can also be recognized at Poljšica pri Podnartu (Fig. 1). First scientific researches of these beds were carried out in the 19th century (MORLOT, 1850; LIPOLD, 1857; Fuchs, 1874; Kinkelin, 1890; Oppenheim, 1896). These early researches focused on macrofossils and the question of the strata's age. Micropaleontological researches have later been made (among others) by PAPP (1959), PAVLOVEC (1961), CIMER-MAN (1967, 1969), PAVŠIČ (1983, 1985) and BRICL and Pavšič (1991). Some of the corals from this locality were also mentioned by BARTA-CALMUS (1973) and some recent reports on macrofossils have been made especially by MIKUŽ (1999, 2002, 2006a, 2006b).

During the years 2006 and 2008, research on non-geniculate coralline red algae (Rhodophyta, Corallinales) from the Gornji Grad beds from Poljšica pri Podnartu was done by the author. Corallines are quite abundant at this locality, but until now more attention was being paid to the fossil algal assemblage from the Gornji Grad area (BASSI & NEBELSICK, 2000; BASSI et al., 2000).

This paper summarizes the author's research from Poljšica and deals with: (1) the systematic description and identification of non-geniculate coralline red algae from Poljšica pri Podnartu and (2) the analysis of the coralline red algal assemblage in the section, with focus on the palaeoenvironmental implications.

Material and methods

Preliminary research of the profile has shown that the corallines are notably present in five layers. Patchy outcrops allow limited sampling area, so the term "horizon" is used here rather than laver. Thus, four horizons (namely A, B, C and D) were sampled. Horizons A and C comprise practically the whole thickness of their layer, whereas the horizon B is limited to the lowermost meter, and the horizon D to the lower and middle part of its layer. The fifth layer with corallines lies immediately below the horizon C and is lithologically indistinguishable from it. Out of several kg of rock samples, 142 thin sections (59 for horizon A, 19 for B, 40 for C and 24 for D) of size 48x28 mm were made and investigated using optical microscope Jenapol Amplival pol U (Carl Zeiss). Photographs were taken with an Axiocam HRc digital camera mounted on an Axioplan 2 optical microscope. Coralline genera were determined according to Braga et al. (1993), Braga and Aguirre (1995), BASSI (1995) and RASSER and PILLER (1999). Dunham's textural classification was used for the general description of limestones (DUNHAM, 1962). Each thallus was measured and surface area for every genus was calculated, rather than using point counter, as it was necessary to distinguish between algal genera in order to determine the composition of algal assemblage for each horizon. Indeterminable thalli were also recorded.

In data interpretation, relative proportions for each horizon were used, in order to avoid differences in investigated surface areas. Biasing, that could result from the differences in thalli forms, as well as from the differences in number of thin sections, has been checked for by calculating probability of presence in thin section for each genus (number of thin sections of a certain horizon with genus *X*, divided by a total number of thin sections of the same horizon).

All the thin sections, along with rock samples, are stored at the Department for Geology, Faculty of Natural Sciences and Engineering, University of Ljubljana, under inventory number 6987.

Lithostratigraphic column

Composite lithostratigraphic column of the Paleogene beds from Poljšica pri Podnartu was constructed from five partly uncovered profiles. These could be linked laterally with the use of morphologically more pronounced and marker layers.

Five main microfacies types can be recognized within the limestones:

Coral fragments - miliolid microfacies is characterized by the dominance of coral fragments (up to 50 %), which are most often heavily encrusted by coralline algae, and large number of miliolids,

though these contribute little to the whole rock (up to 10 %), because of their relatively small size. Coralline algal debris, other foraminifera (especially textulariids and encrusting foraminifera), ostracods, mollusc, rare echinoderm and serpulid fragments are subordinate components. Other fossils (sponge spicules, bryozoans, genicula of green and red algae) are rare. Texture is rudstone/ floatstone with packstone matrix.

Coral fragments – miliolid – coralline algal microfacies is similar, except that the coralline algae join the main constituents. They are present as smaller branched forms or fragments of variable sizes.

Coral fragments – coralline algal microfacies is characterized by coral fragments, often encrusted with coralline algae, and whole or fragmented thalli of coralline red algae. Other fossils are rare (1-2 miliolids per thin section, foraminifera, serpulid, echinoderm and mollusc fragments, fish teeth, ostracods, bryozoans). Texture is rudstone/ floatstone, with wackestone matrix.

Coralline algal microfacies is dominated by planar, several cm^2 large non-geniculate coralline red algae. This microfacies is quite rare, very limited in range and found next to the coral fragments – coralline algal microfacies (though the opposite is not true). Texture is bindstone. Other fossils are present as debris.

Coral fragments microfacies is floatstone/rudstone with wackestone or mudstone matrix. Almost solely coral fragments are present, encrusted by coralline red algae or rarely by bryozoans. Other fossils (miliolids, ostracods, coralline algal, mollusc and serpulid fragments, sponge spicules) are very rare.

Lithostratigraphic column (Fig. 2) begins with weakly lithified mud-supported conglomerates and pebbly-sandy mud of the so-called Basal unit (HEMLEBEN, 1964; BRUCH, 1998; NEBELSICK et al., 2000; SCHMIEDL et al., 2002). Pebbles are well rounded and well sorted. They mostly derive from the Middle Triassic (Ladinian) basement. Some meters wide scours are common, some with graded bedding. No fossils were found at Poljšica. The thickness of the Basal unit at Poljšica can be estimated to over 200 m. It lies discordantly over the Ladinian basement (GRAD & FERJANČIČ, 1976; RAMOVŠ, 1983).

The Basal unit is overlain by an 18 m thick complex of shallow marine sedimentary rocks, named the Gornji Grad beds (HEMLEBEN, 1964; BRUCH, 1998; NEBELSICK et al., 2000; SCHMIEDL et al., 2002). Their slow transgression is marked by a pebbly floatstone/rudstone. Several cm long fragments of a coral *Stylophora* cf. *conferta* (BARTA-CALMUS, 1973) parallel to the bedding are characteristic. Many fossil molluscs are present.

Sandy mud and mudstone follow, with gradual bedding from pebbly silt to clay, and then several layers of limestones, which are especially rich in fossils. The first is marly limestone, floatstone/rudstone with molluscs, fragmented plant remains, nummulitids and ichnofossils (mostly vertical burrowing and ichnogenus *Teredo*). Some rare corallines were found in the uppermost part of this layer. Floatstone/rudstone with packstone matrix that follows contains 10.1 % of corallines.



Fig. 2. Composite lithostratigraphic column of the Oligocene beds of Poljšica pri Podnartu.

Sl. 2. Kompozitni litostratigrafski stolpec oligocenskih plasti V Poljšici pri Podnartu. Grains of quartz are abundant. They are fine grained, very well sorted but angular in shape.

Coral fragments – miliolid and coral fragments – miliolid – coralline algal microfacies are present. This layer was sampled as horizon A (Fig. 2).

Horizon B comprises the lower part of the next layer- floatstone/rudstone with wackestone matrix with many irregular internal erosional surfaces and lenses of sandy silt. Corals are very common in the lower part of this bed and bafflestone is somewhere present. Coralline algae (13.5 %) mostly encrust redeposited coral fragments (coral fragments – coralline algal microfacies) or are themselves fragmented. Number of quartz grains drops significantly.

Next two layers (the upper one sampled as horizon C) contain 21.8 % of non-geniculate corallines, which are apparently preserved in situ. Floatstone/rudstone with packstone and wackestone matrix is again rich in quartz grains, miliolids and molluscs. Ostracods, encrusting foraminifera and echinoderms are also present. Coral fragments – miliolids – coralline algal (though with somewhat less miliolids than in the horizon A) and coralline algal microfacies prevail.

The last carbonate layer (horizon D) in the Gornji Grad beds is similar in appearance to horizon B (Pl. 1, Fig. 1), but has even less fossils. Corallines represent 9.4 % of the rock. Only coral fragments microfacies is present.

Gornji Grad beds end with fine grained muddy quartzy-lithic sandstone with plant fragments and poorly preserved bivalves, and middle grained quartzy-lithic sandstone without macro fossils. This sandstone gradually passes into marine marlstone or the Tegel unit (HEMLEBEN, 1964; BRUCH, 1998; NEBELSICK et al., 2000; SCHMIEDL et al., 2002). The Tegel unit here contains nanoplankton of the Lower Oligocene NP 23 biozone (PAVŠIČ, 1983, 1985; BRICL & PAVŠIČ, 1991). Foraminifera are also very common (CIMERMAN, 1967) and some plant remains can be found (CIMERMAN, pers. com.).

Non-geniculate coralline red algae

Non-geniculate coralline red algae in the sampled horizons (Fig. 2) vary in size and form, as well as in proportions of the genera. Corallines of the horizon A are the smallest, measuring typically less than 100 µm. They are present as fragments, small arborescent forms, encrusters or rarely as free growing planar plants. In the horizon B they mostly encrust coral fragments or are themselves fragmented. Non-geniculate corallines of the horizon C are preserved as several cm² large, free growing crusts parallel to the bedding plane. They are also accompanied by fragments, arborescent thalli and warty to lumpy overgrowths of coral fragments. Corallines of the horizon D are present only as thin encrusters of fragmented corals and clearly redeposited thalli (Pl. 1, Fig. 4). Thalli in all horizons are best ascribed to maërl -"small thalli, especially those that are twig-like" (FOSTER, 2001, 659).

Genera Lithoporella and Neogoniolithon are present in encrusting, layered or foliose forms. Spongites, Lithothamnion and Mesophyllum are encrusting to fruticose, and Sporolithon warty to fruticose. It should be noted here that fruticose forms are in thin sections indistinguishable from arborescent, so the latter are certainly also present.

Encrustations of coral fragments are monospecific (*Lithothamnion* and *Spongites* in the horizon D) or multispecific (*Lithoporella*, *Spongites*, *Lithothamnion* and *Mesophyllum* in horizons A, C and to some extent in B). Competition with encrusting foraminifera for space/substrate is common. *Mesophyllum* and *Neogoniolithon* often form planar thalli, which were growing attached to the sea floor with cell adhesion (Pl. 1, Fig. 2) (WOELKERLING, 1988). *Lithothamnion* and *Spongites* are also common in free growing, unattached arborescent forms.



Fig. 3. Ratios of the non-geniculate coralline red algal genera in the sampled horizons and in the total sample.

Sl. 3. Razmerja med rodovi nečlenjenih koralinej v vzorčevanih horizontih in skupnem vzorcu.

Coralline assemblage markedly differs among the horizons, as is shown in Fig. 3. The most common genus is *Mesophyllum*, followed by *Sporoli*thon and Lithothamnion. Spongites, Lithoporella and *Neogoniolithon* represent minor part in the assemblage. As these proportions are based on measurements of the surface area, they must be considered with great caution, because great differences may arise solely because of the different morphologies of the thalli – most evident example is genus *Lithoporella*, which has thin, often monolayered thallus. Thus it was necessary to calculate the probability for each genus to appear in a thin section of a certain horizon. It turnes out that Lithoporella is indeed very common (43, 47 and 41 % probability), but the differences in probabilities are insignificant enough and its share is approximated to be constant and thus not important in later interpretation. Probabilities of the other genera match very well with the surface proportions, which prove the validity of this data.

Proportions of the indeterminable thalli (thalli which do not contain characteristic structures –



Fig. 4. Ratios of present subfamilies of the non-geniculate corallines in the sampled horizons and in the total sample.
Sl. 4. Razmerja med poddružinami nečlenjenih koralinej v vzorčevanih horizontih in v skupnem vzorcu.

mostly sterile ones, or which are too fragmented) also vary: 43.7 % of the thalli in the horizon A, 22.3 % in B, 22.3 % in C and 30.9 % in the horizon D. Proportions of fragmented thalli are believed to be some sort of auxiliary indicator for the degree of redeposition, which is also connected to the water energy and the distance of the transport.

Differences between the horizons can be also seen on the subfamily level (Fig. 4). *Lithoporella*, *Neogoniolithon* and *Spongites* are assigned to the subfamily Mastophoroideae (family Corallinaceae), *Lithothamnion* and *Mesophyllum* to the subfamily Melobesioideae (family Hapalidiaceae) and *Spongites* to the family Sporolithaceae (WOE-LKERLING, 1988; VERHEIJ, 1993; HARVEY et al., 2003). The similarity of the horizon C to the total sample should be noted.

Discussion

The Paleogene beds from Poljšica pri Podnartu were deposited during a long term eustatic sea level rise, accompanied with a tectonic subsidence of the area, which resulted in the formation of the Slovenian Paleogene Basin, which is a part of the Central Paratethys (RögL, 1998; NEBELSICK et al., 2000; SCHMIEDL et al., 2002). This is why we can observe transition from the proximal (Basal unit) to more and more distal environment (Tegel unit) (SCHMIEDL et al., 2002). Similar development can be found in the Northern Slovenia to the west as far as Bohinj (HERLEC, 1985) and to the east (e.g. HEMLEBEN, 1964; BASSI & NEBELSICK, 2000).

The Gornji Grad beds with its diverse and abundant marine fossil fauna in sandy and marly limestones indicate mesotrophic environment with enough oxygen in the water column and large terrigenous input. The later probably hindered the growth of a larger and uniform coral ridge (SCHMIEDL et al., 2002) and only small coral bioherms can thus be found. Large terrigenous input and large amount of organic matter were also the cause for reducing oxygen level below the sediment-water interface. Coralline red algae, molluscs, benthic foraminifera and corals were the main carbonate producers.

The Gornji Grad beds are a heterogenous unit and the lithological changes through the lithostratigraphic column are here interpreted as facies changes, which could be caused by several reasons (changes in sea currents, sea-bottom configuration, amount of terrigenous input, shifting of a river mouth etc.) and not necessarily by the deepening of the sea.

Coral fragments – miliolids and coral fragments – miliolids – coralline algal microfacies of the horizon A probably correspond to the foraminiferal – coralline algal facies of BASSI and NEBELSICK (2000) and coralline algal debris facies (NEBELSICK et al., 2005) from the Gornji Grad area. NEBEL-SICK et al. (2005) assigned this facies to the inner to middle shelf environment. Nearshore environment is also championed by very well sorted, but angular grains of quartz, the highest percentage of fragmented corallines and the packstone matrix.

Layer with the horizon C has somewhat less miliolids and quartz grains. Wackestone matrix is also common, which indicates quieter environment. This is also supported by the lowest degree of fragmentation and corallines preserved in situ. Coralline red algae are also the most abundant in this horizon. This layer was deposited offshore, where normal marine conditions prevailed, though the influence of the hinterland was still strong. The presence of coralline algal microfacies (coralline algal facies *confer* BASSI and NEBELSICK (2000) and crustose coralline algal facies *confer* NEBELSICK et al. (2005)) also points to the middle shelf environment (NEBELSICK et al., 2005).

Layers with the horizons B and D were deposited under strong influence of storm waves, in the middle part of the mixed carbonate-siliciclastic ramp. Coral facies was also recognized by BASSI and NEBELSICK (2000) and NEBELSICK et al. (2005). The latter assign it to the middle shelf, but direct comparisons must not be made, because here observed corals obviously underwent some transport.

Coralline red algae were mostly redeposited and their assemblages must be regarded cautiously. In situ corallines of the horizon C represent one source area from which thalli were shed into other parts of the ramp. Corallines of the horizons A, B and D are not preserved in situ, yet they give some information about the second source area. This is best viewed in the horizon D, where almost solely coral fragments overgrown with corallines can be found. The second source areas were small coral bioherms, where fragile ramiform corals were being destroyed during periods of agitated water (storms) and their fragments redeposited, along with all the epiphytic organisms they hosted. Out of 12-16 kg of isolated, several cm large coral fragments collected from the weathered horizon B, nearly half were encrusted, and never on the surface of breakage, which proves that corals were encrusted already during their growth.

Coralline red algae assemblage in the first source area consists of all six genera and the diversity is the highest. This can be explained by various types of substrate available (NEBELSICK et al., 2000). *Mesophyllum* and *Neogoniolithon* were able to attach on the sandy-muddy bottom and develop extensive thalli. Sporolithon is also often present in free growing arborescent forms, while Lithothamnion is quite rare (it also has low probability for this horizon). The second source area (coral bioherms) contains less diverse assemblage, where Lithothamnion prevails. Mesophyllum is rare and Neogoniolithon even absent, because of the lack of appropriate substrate. Interestingly, Lithoporella is altogether absent here. Possible explanation could be the intraspecific competition with Lithothamnion, which was evidently more successful as the first encruster. Coral particles in other horizons contain richer assemblages, probably due to several years of growth and more mature community, as several generations of the same genus, as well as several other genera are usually present (Lithoporella being among them). Coralline assemblages in the horizons A and B are a result of mixing of thalli from both (possibly even more) source areas. A small proportion of thalli probably grew in situ.

Non-geniculate corallines have, as most other groups of organisms, undergone notable changes in their development (AGUIRRE et al., 2000) and we must be careful in interpreting palaeoenvironment using observations of the modern flora. However, some implications will be given. In the Lower Oligocene melobesioids and lithophylloids/mastophoroids were prevailing over sporolithaceans (AGUIRRE et al., 2000) and their relationships are markedly different from the ones observed in the Gornji Grad beds, so some environmental control was evidently present. Melobesioids and sporolithaceans prevail in the horizon C and in the total sample. This situation can be seen in recent environments in deeper waters in lower altitudes. Mastophoroids are also present in the Gornji Grad beds and they tend to occupy shallower waters of lower altitudes (Adey & Macintyre, 1973; Aguirre et al., 1993). However, deeper water genera can also occur in cryptic environment, such as shallow muddy water because of the large terrigenous input certainly was. Melobesioids are more abundant on the coral bioherms, which could be because of the clearer water further away from the shore. Warm subtropical or tropical waters were also championed by HERLEC (1989) and SCHMIEDL et al. (2002).

Conclusions

The Lower Oligocene Gornji Grad beds from Poljšica pri Podnartu were deposited in the inner and middle part of a carbonate-siliciclastic ramp in a mesotrophic marine environment with welloxygenated water and substantial terrigenous input.

Limestones with non-geniculate coralline red algae were deposited in a high-energy nearshore environment, in a more distal and quieter normal marine environment, or under strong influence of storm waves.

Two source areas from which corallines were shed into other parts of the ramp are sandy-muddy bottom and small coral bioherms with its epiphytic organisms. The first has higher coralline diversity and corallines were able to grow on a variety of substrates, forming also planar crusts on the sea floor. Mesophyllum and Sporolithon are the most prominent genera here. Neogonio*lithon* and *Lithoporella* are here more abundant than elsewhere. Lithothamnion and Spongites are rare. Lithothamnion prevails in the second source area, where limited diversity was observed. Lack of appropriate substrate strongly hindered the growth of the genus Mesophyllum and Neogonio*lithon* - the later is even totally absent, as well as *Lithoporella*, whose non-appearance could be related with Lithothamnion being a more successful primary encruster. *Spongites* is also quite abundant, while Sporolithon is rare.

Coralline assemblage on a subfamily level corresponds to the tropical or subtropical conditions in somewhat cryptic environment because of the large terrigenous input. In more distal environment with clearer water, melobesioids strongly prevail over sporolithaceans.

Systematic palaeontology

Research of coralline red algae in Slovenia scarcely has any history, and though many authors (for example Kinkelin, 1890; Grad & Ferjančič, 1976) mention them in their work, few have given them more consideration (ANIČIĆ & OGORELEC, 1996; GALE, 2006; OTONIČAR & CIMERMAN, 2006). Likewise, the potential of this group in palaeoenvironmental and sedimentological studies has been largely ignored. It has been only recently that BASSI et al. (2000) and BASSI and NEBELSICK (2000) have done some thorough study on the systematic palaeontology of corallines from the Gornji Grad area, where abundant corallines can be found in the Gornji Grad beds, where somewhat different sedimentological succession from the one at Poljšica is encountered.

Recent studies on fossil coralline red algae are focused on features that were believed for a long time to be too obscured by fossilization to be of any use (WRAY, 1977). Determination of fossil genera was thus based on the: (1) type and location of reproductive structures, (2) character of the hypothallium (part of the thallus where cell filaments are oriented more or less parallel to the substrate), (3) character of the perithallium (where cell filaments are perpendicular to the substrate), and (4) presence or absence of trichocytes (specialized, hair-producing cells, usually larger than adjacent vegetative cells and with thicker cell walls (WOELKERLING, 1988)) and their character (WRAY, 1977).

With improvements in the analytical techniques it became clear that, despite fossilization processes, it is sometimes still possible to observe many features that are used by biologists in distinguishing between recent species (BOSENCE, 1991; BRAGA et al., 1993), and type material of the fossil corallines is thus still under revision (BRAGA et al., 1993; BRAGA & AGUIRRE, 1995; AGUIRRE & BRAGA, 1998; Rasser & Piller, 1999; Bassi et al., 2000; Vannucci et al., 2000; Quaranta et al., 2007).

Modern descriptions emphasise filamentous construction of the thallus, so the terms hypothallium and perithallium are no longer used. Thallus can have dorsiventrally (dorsal and ventral side are distinct from each other) or radially arranged filaments. Genus Tenarea can be isobilateral. In dorsiventral arrangement monomerous and dimerous constructions are further distinguished. Monomerous thalli consist of one group of filaments (Fig. 5 A. B). The lower part is subparallel to the thallus surface and is called the core. The core can be coaxial (cells of adjacent filaments are arranged in tyres) or non-coaxial (plumose). Filaments of the core region curve outwards to form the periphery, where the filaments are more or less perpendicular to the thallus surface. Dimerous thalli are constructed from two groups of filaments that are perpendicular to each other (Fig. 5 C). The ventral group is called the primigenous layer, whilst the dorsal filaments form the postigenous layer (WOELKERLING, 1988). Successive cells of the same filament are connected by primary pores and the cells of adjacent filaments can be linked by secondary pores or by more extensive

cell fussion (Fig. 5 D) (WRAY, 1977; WOELKERLING, 1988). Epithallial layer covers the surface of the thallus (Fig. 5 D, E) (WRAY, 1977; WOELKERLING, 1988).

Very important for the coralline genera determination are their reproductive structures (sporangia), developed inside sporangial chambers, which are most often grouped in one larger chamber, called conceptacle. Corallines can reproduce sexually or asexually. Sexual conceptacles are always uniporate (i.e. they have only one pore in the conceptacle roof) (Fig. 5 I). Asexual (tetra/bisporangial) conceptacles can be uniporate (Fig. 5 F) or multiporate (Fig. 5 G), and are considered more common in fossil forms. Sporangial chambers of the family Sporolithaceae remained calcified and separated from each other, and are grouped in sorus (plural sori) (Fig. 5 H). They are separated by calcified filaments termed paraphyses (WOELK-ERLING, 1988; RASSER & PILLER, 1999; VANNUCCI et al. 2000).

Coralline red algae from the limestones of the Gornji Grad beds from Poljšica pri Podnartu have been assigned to six genera, which were also recognized in the Gornji Grad area (BASSI & NEBEL-SICK, 2000). These are: *Lithoporella* (Foslie) Foslie



Fig. 5. Some vegetative and reproductive structures of the coralline red algae. A–C: organization of the thallus filaments and the subdivisions of the thallus; D: details of the peripheral part of the monomerous thallus; E: flared epithallial cells; F–I asexual and sexual reproductive structures. Modified after RASSER and PILLER (1999).

Sl. 5. Nekatere vegetativne in razmnoževalne strukture koralinej. A–C: organizacija celičnih filamentov in poimenovanje različnih delov talusa; D: detajli perifernega dela monomernih talusov; E: plamenaste epitalijalne celice; F–I: nespolne in spolne razmnoževalne strukture. Prirejeno po RASSER in PILLER (1999). 1909, Neogoniolithon Setchell & Mason 1943, Spongites Kützing 1841, Lithothamnion Heydrich 1897 nom. cons., Mesophyllum Lemoine 1928 and Sporolithon Heydrich 1897. Some differences from the two locations have been observed on the species level (GALE, in preparation).

Genera can be distinguished on the basis of observations of the above mentioned vegetative and reproductive structures. Only brief descriptions of these genera are given here, as the determination on the species level exceeds the scope of this paper. Taxonomic subdivision of the order Corallinales follows AGUIRRE et al. (2000) and HARVEY et al. (2003). Because of the ongoing revision of the type material for many coralline species, open nomenclature had to be adopted for some.

Division **Rhodophyta** Wettstein, 1901 Class **Rhodophyceae** Rabenhorst, 1863 Order **Corallinales** Silva & Johansen, 1986 Family **Corallinaceae** Lamouroux, 1812 Subfamily **Mastophoroideae** Setchell, 1943

Description: Thallus is non-geniculate; some cells of adjacent filaments are connected by cell fusion. Sporangia develop in uniporate conceptacles (WOELKERLING, 1988).

Genus *Lithoporella* (Foslie) Foslie, 1909 Pl. 1, Fig. 7; Pl. 2, Fig. 3

Description: Plants are non-geniculate and grow freely or attached to the surface. Thallus can be encrusting to foliose, usually without vertical protuberances. Construction of the thallus is dorsiventral and dimerous. Primigenous filaments consist of palisade cells. Postigenous filaments are rarely developed, usually only around conceptacles, which are uniporate and without columella. Conceptacle roof is several cell layers thick. Cell fusion is common and clearly visible (WOELKERLING, 1988).

Remarks: One species (Lithoporella melobesioides (Foslie) Foslie 1909) of this genus was recognized from Poljšica pri Podnartu. L. melobesioides is a well known fossil and recent species with global distribution (WOELKERLING, 1988; STU-DENCKI, 1988; BASSI, 1995, 1998; RASSER & PILLER, 1999; AGUIRRE et al., 2000; BASSI & NEBELSICK, 2000; RASSER & NEBELSICK, 2003; PAYRI & CABIOCH, 2004).

Genus Neogoniolithon Setchell & Mason, 1943 Pl. 1, Fig. 2

Description: Plants are non-geniculate, epigenous or growing freely. Thallus is encrusting to fruticose, organization of cell filaments dorsiventral and monomerous. Core is coaxial. Epithallial cells are rounded or flattened, but not flared. Asexual conceptacles are uniporate, with roof several cell layers thick. Cells are connected by cell fusion. Columella is sometimes present (WOE-LKERLING, 1988).

Remarks: Species *Neogoniolithon contii* (Mastrorilli) Quaranta et al. 2007 is known from the

Upper Eocene of Austria (RASSER & PILLER, 1999) and Italy (BASSI, 1998), and from the Lower Oligocene of Slovenia (BASSI & NEBELSICK, 2000) and Italy (FRAVEGA & VANNUCCI, 1987).

> Genus Spongites Kützing, 1841 Pl. 1, Fig. 6

Description: Plants are non-geniculate, epigenous or unattached. Thalli are encrusting to fruticose, filaments dorsiventral and dimerous or monomerous. Cells of the primigenous layer are not palisade. Core is non-coaxial. Epithallial cells are rounded or flattened, but not flared. Some cells of adjacent filaments are connected by cell fusion. Asexual conceptacles are uniporate. Conceptacle roof is several cell layers thick. Columella can be present (WOELKERLING, 1988).

Remarks: Spongites sp., which was found at Poljšica, is also known from the Upper Eocene of Austria (RASSER & PILLER, 1999) and Lower Oligocene of Slovenia (BASSI & NEBELSICK, 2000).

Family **Hapalidiaceae** Harvey et al., 2003 Subfamily **Melobesioideae** Bizzozero, 1885

Description: Thallus is non-geniculate. Some cells of adjacent filaments are connected by cell fusion. Asexual conceptacles are multiporate (WOELKERLING, 1988).

Genus *Lithothamnion* Heydrich, 1897 nom. cons. Pl. 1, Fig. 7; Pl. 2, Fig. 1

Description: Plants are non-geniculate, epigenous or unattached. They vary in shape from encrusting to fruticose. Thallus is dorsiventrally organized and monomerous, with non-coaxial core. Epithallial cells are flattened and flared. Cell fusion is present. Asexual conceptacles are multiporate and lack columella. Conceptacle roof is thick (WOELKERLING, 1988).

Remarks: Three species of this genus were found, known also from the Upper Eocene to Lower Miocene beds of Southern and Middle Europe, as well as from the Middle East (STUDENCKI, 1988; BASSI, 1995; BASSI & NEBELSICK, 2000).

Genus Mesophyllum Lemoine, 1928 Pl. 1, Fig. 7; Pl. 2, Fig. 2, 4, 5

Description: Plants of this genus are non-geniculate, epigenous or unattached. Thallus is encrusting to fruticose. Organization of filaments is dorsiventral and monomerous, with coaxial core. Some conceptacles are connected by cell fusion. Asexual conceptacles are multiporate, with thick roof. Columella is absent (WOELKERLING, 1988).

Remarks: Three species of this genus were found at Poljšica. Two of them are already known from the Paleogene beds (both also from the Gornji Grad area (BASSI & NEBELSICK, 2000)), whilst the third could not be ascribed to any known species of this genus.

Family **Sporolithaceae** Verheij, 1993 (Subfamily **Sporolithoideae** Setchell, 1943)

Description: Non-geniculate, almost completely calcified thallus. Cells of adjacent filaments are connected also by cell fusion (RASSER & PILLER, 1999). Sporangia are grouped in sori (VANNUCCI et al., 2000).

Genus Sporolithon Heydrich, 1897 Pl. 1, Fig. 5, 6; Pl. 2, Fig. 7

Description: Plants are non-geniculate, epigenous or grow unattached. Thallus is encrusting to fruticose. Filaments are organized dorsiventrally and monomerous, with non-coaxial core. Epithallial cells are flattened and flared. Cell fusion is present. Sporangia are separated by calcified filaments – paraphyses (WOELKERLING, 1988). Sporangial chambers are grouped in sori (VANNUCCI et al., 2000).

Remarks: Sporolithon cf. *statiellense* (Airoldi) Vannucci et al. 2000 is also known from the Oligocene of Italy and Germany (VANNUCCI et al., 2000; RASSER & NEBELSICK, 2003). *Sporolithon* sp. 1 from the Upper Eocene of Austria (RASSER & PILLER, 1999) is now known also from Poljšica pri Podnartu.

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Plate 1 – Tabla 1

- 1 Limestone with numerous internal erosional surfaces of the horizon D. Apnenec horizonta D s številnimi notranjimi erozijskimi površinami.
- 2 Genus *Neogoniolithon* (horizon A) in life position. Scale bar 400 μm. Rod *Neogoniolithon* v življenjskem položaju. Merilo 400 μm.
- 3 Unidentifiable unattached melobesioid in overgrowth with an encrusting foraminifera (A). Seasonal growth is clearly visible. Small borings are present (arrow). Horizon A; scale bar 600 µm. Nedoločljiva nepritrjena koralineja poddružine Melobesioideae v preraščanju s skorjasto foraminifero (A). Sezonska rast je jasno vidna. Puščica kaže na manjše izvrtine v talusu. Horizont A; merilo 600 µm.
- Redeposited thallus of an unidentifiable coralline red alga. Geopetal structure was formed prior to redeposition. Horizon D; scale bar 200 µm.
 Preložen talus nedoločljive koralineje z geopetalno teksturo, ki je nastala še pred preložitvijo. Horizont D; merilo 200 µm.
- 5 Sporolithon is growing on a coral (C) fragment and is itself eroded (arrow) and overgrown by a melobesioid. Horizon B; scale bar 450 µm. Sporolithon raste na korali (C). Talus je delno erodiran (puščica) in prerasel s koralinejo poddružine Melobesioideae. Horizont B; merilo 450 µm.
- 6 The same thallus as in figure 5, with large borehole. Small ovoid structures (arrow) are sporangial compartments. Horizon B; scale bar 450 μm. Isti talus kot na sliki 5 z veliko izvrtino. Drobne jajčaste strukture (puščica) so sporangijski prostori. Horizont B; merilo 450 μm.
- 7 Coral fragment (C) overgrown by several different non-geniculate coralline red algae (possible even more generations of the same species are present). From bottom to top: ?Lithothamnion sp. (L), Lithoporella sp. (P) and Mesophyllum sp. (M). Arrow points at the tetra/bosporangial conceptacle of Lithoporella. Mesophyllum partly grows on a sediment, which indicates that the coral fragment was already lying on a sea floor, when Mesophyllum started to grow over it. Horizon A; scale bar 300 µm.

Koralni fragment (C) prerašča več rodov nečlenjenih koralinej (verjetno je prisotnih celo več generacij iste vrste). Od spodaj navzgor: ?*Lithothamnion* sp. (L), *Lithoporella* sp. (P) in *Mesophyllum* sp. (M). Puščica kaže na tetra/bisporangijski nespolni konceptakel roda *Lithoporella*. *Mesophyllum* delno raste preko sedimenta, iz česar lahko sklepamo, da je koralni fragment že ležal na dnu, ko ga je začela obraščati omenjena alga. Horizont A; merilo 300 µm.

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Plate 1 – Tabla 1



Plate 2 – Tabla 2

1 *Lithothamnion* sp. is growing on a coral (C). Geopetal structure (G) points towards upper right of the picture. Multiporate conceptacles and seasonal growth (banding) are clearly visible. Horizon A; scale bar 650 μm.

Lithothamnion sp. raste na korali (C). Geopetalna tekstura (G) kaže proti desnemu zgornjemu kotu slike. Dobro so vidni mnogoporni konceptakli in sezonska rast talusa (pasnat periferni del). Horizont A; merilo 650 µm.

- 2 Mesophyllum sp. with multiporate conceptacle. Pores are visible in the conceptacle roof (arrow). Slightly oblique section; horizon A; scale bar 250 µm. Mesophyllum sp. z mnogopornim konceptaklom. V strehi konceptakla so vidne pore (puščica). Rahlo poševen presek; horizont A; merilo 250 µm.
- 3 *Lithoporella melobesioides* (Foslie) Foslie 1909 with foliose thallus, growing on a coral. Arrow points at the cell fusion. Postigenous filaments are developed around uniporate conceptacles. Horizon A; scale bar 400 μm.

Lithoporella melobesioides (Foslie) Foslie 1909 z listnatim talusom raste na korali. Puščica kaže na celično fuzijo. Okrog monopornih konceptaklov so razviti postigeni filamenti. Horizont A; merilo 400 µm.

- Foliose Mesophyllum with umbrella type porosity. Cavity beneath the thallus is filled with calcite cement and pelloids. Horizon A; scale bar 400 µm.
 Listnat Mesophyllum z dežnikasto poroznostjo. Prostor pod talusom je zapolnjen s kalcitnim cementom in peloidi. Horizont A; merilo 400 µm.
- *Mesophyllum* sp. growing partly on a coral and partly on substrate. Coaxial core is visible. Horizon A; scale bar 500 µm.
 Mesophyllum sp. raste delno na korali in delno na sedimentu. Koaksialno jedro je lepo vidno. Horizont A; merilo 500 µm.
- 6 Spongites sp. with non-coaxial core and uniporate conceptacle with columella. Horizon D; scale bar 100 µm.

Spongites sp. z nekoaksialnim jedrom in monopornim konceptaklom s kolumelo. Horizont D; merilo 100 $\mu m.$

7 *Sporolithon* sp. in transverse section. Arrow points at sporangial chamber. Horizon A; scale bar 300 μm.

Sporolithon sp. v prečnem preseku. Puščica kaže na sporangijske prostore. Horizont A; merilo 300 μm.

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Plate 2 – Tabla 2



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