CALCAREOUS ALGAE FROM THE LOWER OLIGOCENE GORNJI GRAD BEDS OF NORTHERN SLOVENIA

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Riassunto. In questo lavoro vengono presentati i primi risultati riguardanti le alghe calcaree degli "strati di Gornji Grad" (Oberburger Schichten *Auctorum*) attribuiti all'Oligocene inferiore della Slovenia settentrionale. Le Corallinaceae sono rappresentate da sette generi (*Lithoporella, Neogoniolithon, Spongites, Lithothamnion, Mesophyllum, Sporolithon, Subterraniphyllum*). Sono inoltre presenti i generi *Polystrata* (Peyssonneliaceae), *Halimeda* (Halimedaceae) e *Cymopolia* (Dasycladaceae).

Una rigorosa interpretazione tassonomica degli esemplari fossili di corallinacee secondo i caratteri diagnostici applicati in ficologia, sia a livello di genere che di specie, non è sempre possibile. Le limitazioni poste dalla difficoltà di applicare la sistematica delle specie viventi a quelle fossili e dall'assenza di studi comparativi con i tipi nomenclaturali, impediscono di avanzare conclusioni tassonomiche definitive per i taxa esaminati. Pertanto la maggior parte delle specie sono state identificate in nomenclatura aperta in attesa di revisioni tassonomiche delle specie fossili già note in letteratura. Lo studio delle morfologie di crescita algale ha evidenziato, sia a livello di genere che di specie, un'ampia variabilità tipologica.

Abstract. This paper presents the first systematic account of calcareous algae from the limestones of the Lower Oligocene Gornji Grad beds of northern Slovenia. These bioclastic limestones are dominated by different coralline algal assemblages as well as corals, large and small benthic foraminifera as well as bivalves. The taxonomy and growth-forms of eleven species of seven non-geniculate coralline algal genera are described: *Lithoporella, Neogoniolithon, Spongites, Lithothamnion, Mesophyllum, Sporolithon, Subterraniphyllum*. Additionally, the genera *Polystrata* (Peyssonneliaceae), *Halimeda* (Halimedaceae), and *Cymopolia* (Dasycladaceae) are present.

The taxonomic interpretation of fossil coralline material in a manner consistent with generic and specific concepts currently in use for Recent material is, at present, difficult. In the absence of comparative studies on type material, only limited comparisons are possible, and in most cases definitive taxonomic conclusions cannot be reached. Most of the species designations are thus made following an open nomenclature pending the rigorous taxonomic revision of historically established, fossil coralline algal species. The present study reveals a considerable variation of growth-form morphologies at both genus and species levels. This demonstrates the difficulties in using this feature as a diagnostic character in the identification of fossil coralline red algal taxa.

Introduction.

Calcareous algae are important constituents of Tertiary shallow water carbonates and are abundantly represented as an important sediment contributor in a variety of depositional environments. The flourishing of coralline red algae (Corallinales, Rhodophyta) in Oligocene carbonates in the circum-alpine region has been emphasised since the last century (e.g. Suess, 1868; Schwager, 1883; Oppenheim, 1913; Fabiani, 1915; Schweighauser, 1953) often resulting in the designation of these limestones as "Lithothamnienkalk" or "Calcari a Melobesie/Nullipore". Despite their abundance, there have been relatively few publications focusing on the systematic palaeontology of the Oligocene representatives of this group (e.g. Airoldi, 1932; Conti, 1943; Johnson, 1955; Maslov, 1956). Mastrorilli (1958, 1973) described several coralline algal species from the Eocene-Oligocene sediments of the Veneto region of northern Italy. The Oligo-Miocene coralline associations of the Piedmont Basin have also been reported (e.g. Mastrorilli, 1968a; Fravega et al., 1984, 1987, 1988, 1994; Fravega & Vannucci, 1987a; Vannucci et al., 1993, 1996).

A detailed investigation of the Oligocene deposits of the Gornji Grad area in northern Slovenia (Fig. 1) is in progress in order to assess the faunal and floral assemblages and related palaeoenvironments within the framework of the special research program (SFB275) of the German Science Foundation (DFG) "Climate coupled Processes in Mesozoic and Cenozoic Geological Systems" at the University of Tübingen (Germany). The present study represents the first systematic account of the Palaeogene calcareous algae from northern Slovenia. Recent works on fossil coralline red algae have shown that taxonomic criteria currently used by phycologists at

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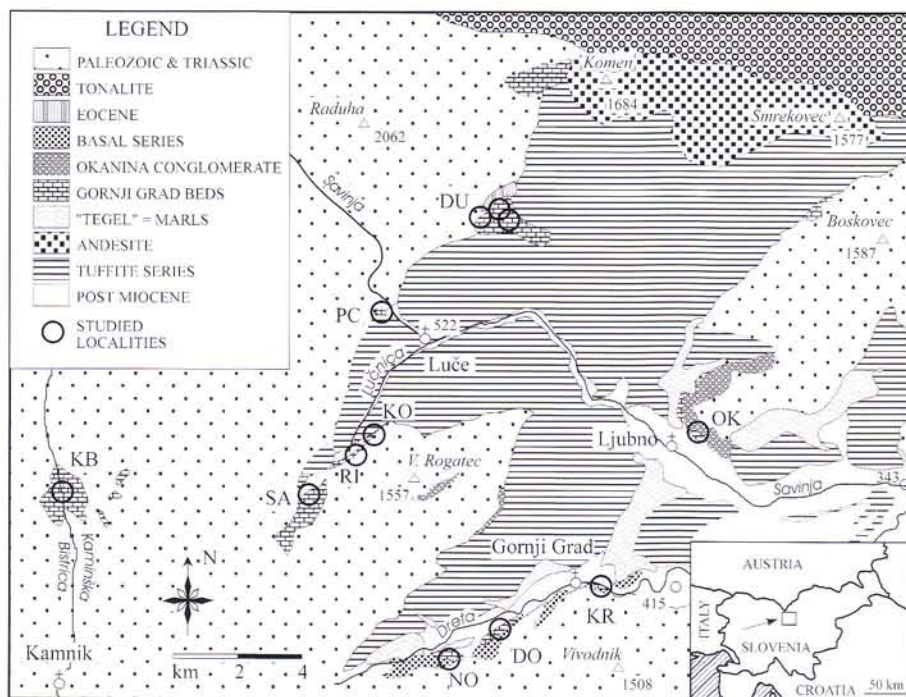
Fig. 1 - Simplified geology and outcrops in the Gornji Grad area, northern Slovenia. KB= Kaminška Bistrica, SA= Sv. Anton, RI= Rihir, KO= Korenovec, PC= Pecovnik, DU= Dupeljnik, NO= Nova Štifta, DO= Dol, KR = Kriznar, OK= Okanina.

delimit species in the Recent corallines are still debated. Detailed studies concerning the Recent genera of Corallinales demonstrate that the stability of the characters used to identify species has never been assessed. For most species, few, or no data are available (Woelkerling, 1985, 1996; Penrose, 1992; Verheij, 1993; Woelkerling & Harvey, 1993; Wilks & Woelkerling, 1995; Townsend et al., 1995).

generic and subfamily levels can be identified in fossil material (see General taxonomic remarks). In this paper, neontological taxonomic concepts for Corallinaceae are applied. This has already been done for fossil coralline red algae from the Late Eocene of Veneto (Bassi, 1995 a, 1998) and Middle-Upper Eocene of Austria (Rasser, 1994; Rasser & Piller, 1999), the Oligocene and Neogene of the Piedmont Basin (Basso et al., 1996, 1997, 1998), as well as from the Neogene of Spain (Braga & Aguirre, 1995).

The Lower Oligocene carbonates of the Gornji Grad area contain a rich flora of well preserved calcareous algae which have yet to be described. This prompted a detailed investigation of which the main aims are: (1) the systematic description and identification of the calcareous algae with particular regard to the non-geniculate coralline algal species; (2) the comparison between these Lower Oligocene coralline species to those others described so far in the literature from the circum-alpine region and southern Europe; and (3) a description of the coralline algal growth-forms in order to assess the variations of growth-form morphologies at both genus and species levels.

General taxonomic remarks.

The taxonomy of fossil coralline red algae (Corallinales, Rhodophyta) is being revised as a consequence of new taxonomic criteria proposed both in the phycological and palaeophycological literature (e.g. Woelkerling, 1988; Braga et al., 1993; Braga & Aguirre, 1995, 1998; Rasser & Piller, 1999). The characters needed to

Recent revisions have clarified the synonymy or the validity of several taxa (e.g. Woelkerling, 1988; Braga et al., 1993; Chamberlain & Keats, 1994). These revisions have furthermore clearly demonstrated that the re-identification of old, established species both for the Recent and fossil material is only possible with the aid of comparative studies with the type collections or with new material from the type localities (Braga & Aguirre, 1995, 1998; Aguirre et al., 1996; Basso et al., 1996, 1998). Studies on fossil calcareous red algae have already shown, however, that taxonomic criteria currently used by phycologists at generic and subfamily levels can be identified in fossil material (Bosence, 1991; Braga et al., 1993; Bassi, 1995a, 1998; Braga & Aguirre, 1995, 1998; Aguirre et al., 1996; Basso et al., 1996). Many representatives of this group have to be reassigned to different genera which so far have not been identified in the fossil material (Moussavian & Kuss, 1990; Braga et al., 1993; Aguirre et al., 1996; Bassi, 1998; Rasser & Piller, 1999). These have also illustrated the risks of using the names of taxa without reassessing their precise circumscription (Aguirre et al., 1996) and confirmed the necessity of avoiding the use of taxa with no preserved type material (Braga & Aguirre, 1998).

The classification of Recent geniculate coralline algal genera is largely based on genicular cell characteristics (the genicula are uncalcified segments between the calcified intergenicula in Corallinales). The position and nature of conceptacles, growth habits and branching modi are also used (e.g. Johansen & Silva, 1978; Woelkerling, 1988, 1996; Riosmena-Rodríguez & Siqueiros-Beltrones, 1996). The inclusion of most fossil species in various geniculate genera of Corallinales by most

authors is based on the supposition that genicula occur (both at points of branching and within branches), even though they have not been observed. In reality, genicula are unknown for most fossil species placed in geniculate coralline genera, and indeed, genicula, as noted by Lemoine (1939), Johnson (1961), Bosence (1991) and Bassi (1998), are seldom preserved in fossil material. In the absence of genicula, the placement of most fossil species into geniculate genera has been based mainly on vegetative features observable in fragments presumed to be segments of geniculate branches. This is evident, for example, in keys to genera published by Lemoine (1970) and Poignant (1979) and in many accounts of species placed in geniculate genera (e.g. Ishijima, 1954, pp. 53-75; Johnson, 1964, pp. 30-36; Mastrorilli, 1968b, pp. 380-388; Lemoine, 1970, pp. 192-193). The assignments of fossil species to geniculate genera must be treated with caution, especially in the absence of further assessments of these fossils in relation to current concepts for geniculate coralline genera (e.g. Johansen, 1976; Womersley & Johansen, 1996a, 1996b, 1996c; Bassi et al., 2000), all of which are based on studies of living species.

The status of the species thus far identified in the Eocene-Oligocene must be checked and verified according to the vegetative characters which are considered valid at genus and species level. According to this taxonomic scenario, some genera and most species herein described from fossil material cannot be rigorously compared to any present-day coralline taxon. Until the taxonomic revision of type material has taken place, an open nomenclature for species identification is used.

Study area and methods.

The study area represents an important transition zone between the northern most extension of the Mediterranean Tethys to the South and the developing Paratethys to the North and East. Although the rich fossil content and facies variations of the Gornji Grad beds are historically well documented (Reuss, 1851, 1864; Morlot, 1853; Rolle, 1857; Stur, 1871; Waters, 1874; Teller, 1885, 1896, 1898), there have been few detailed modern examinations of its fauna, flora as well as microfacies (Hemleben, 1964; Barta-Calmus, 1973; Drobne et al., 1985; Bricl & Pavcic, 1992). The Gornji Grad beds (historically known as the "Oberburger Schichten" *Auctorum*) form part of a highly varied transgressive sequence (Fig. 1). This includes a basal series of terrigenous sediments followed by the Gornji Grad beds described here, overlain by marls rich in foraminifera which are capped by thick series of volcanoclastic tuffs. The Gornji Grad beds themselves consist of both siliciclastics and carbonates of marine origin and can follow above Triassic Limestones, Eocene limestones (Jelen et al., in prep.), the basal terrigenous sediments (see above)

or conglomerates of indeterminate age (possible Eocene). The wide distribution of disjunct outcrops (Fig. 1) reflects the heavy tectonic activity in this area. The stratigraphical framework of the Gornji Grad beds is given by Drobne et al. (1985) who recognized *Nummulites fichteli* and *N. germanicus* indicating an Early Oligocene age. Furthermore, nannoplankton occurring in the marly beds just above Gornji Grad beds indicates the NP 23 zone (upper Early Oligocene; Bricl & Pavcic, 1992).

The carbonates consist predominantly of poorly sorted, biogenic rudstones with a wacke-to packstone matrix; pack- and grainstones are subordinate. The principal components are coralline red algae together with a moderately coral fauna including both solitary and colonial forms. Large and small benthic foraminifera as well as calcitic bivalves are also common. Subordinate are gastropods, bryozoans, brachiopods, echinoderms, serpulids, and dasycladalean algae. Seven microfacies were distinguished on the basis of lithologic fabric and component distribution as recognized in thin section analysis: nummulitic, bivalve, foraminiferal-coralline algal, coralline algal, coralline algal-coral, coral, and grainstone facies (a detailed facies description is in preparation).

The nummulitic facies is characterised by packstones dominated by small, highly fragmented nummulites and terrigenous components. Miliolid and rotaliid small benthic foraminifera are also present along with bryozoans, bivalves and rare barnacles. Unidentified coralline algae are rare and very highly fragmented. Highly fragmented and abraded oysters and pectinid bivalves dominated the rudstones of the bivalve facies along with isolated coral, miliolids and textulariids. Unidentified coralline algae are present in moderate amounts.

The fine packstones of the foraminiferal-coralline algal facies are dominated by miliolids and textulariids foraminifera. *Sphaerogypsina* can be common. Common, fragmented coralline algae include *Lithothamnion* sp. 1 and *Mesophyllum* sp. 1.

The rudstones with wacke-to packstone matrix and bindstones of the coralline algal facies is totally dominated by a diverse coralline algae flora. The most characteristic species is *Neogoniolithon* sp. 1 consisting of thick crust 500 µm in thickness and up to several cm long. *Lithoporella melobesioides*, *Spongites* sp. 2, *Lithothamnion* sp. 1, *Mesophyllum* sp. 1 and *Sporolithon* sp. 1 are common. *Spongites* sp. 1, *Lithothamnion* sp. 2, and *Polystrata alba* are also present. Thick algal encrustation sequences can be observed and the components are generally well preserved. Rotaliid small benthic foraminifera are common.

The rudstones with wacke-to packstone matrix of the coralline algal-coral facies are dominated by a diverse coralline algal flora and corals. The coralline algal flora consist of common *Lithoporella melobesioides*, *Spongites*

Family	Subfamily	Genus	Species
Corallinaceae Lamouroux, 1816	Mastophoroideae Setchell, 1943	*Lithoporella*	*melobesioides* (Foslie) Foslie, 1909
		Neogoniolithon	sp. 1
		Spongites	sp. 1
			sp. 2
	Melobesioideae Bizzozero, 1885	*Lithothamnion*	sp. 1
			sp. 2
		Mesophyllum	sp. 1
	Geniculate corallines *sensu lato*		
?	?	*Subterraniphyllum* *	*thomasii* Elliott, 1957
Sporolithaceae Verheij, 1993		*Sporolithon*	sp. 1
Peyssonneliaceae Denizot, 1968		*Polystrata*	*alba* (Pfender) Denizot, 1968
Dasycladaceae (Kützing, 1843) emend. Berger & Kaever, 1992		*Cymopolia*	sp. 1
Halimedaceae Link, 1832		*Halimeda*	sp. 1

Tab. 1   - Calcareous algal genera and species identified in the Lower Oligocene Gornji Grad beds, northern Slovenia. * = genus of uncertain position within the order Corallinales (see text).

sp. 1 and sp. 2, *Lithothamnion* sp. 1, *Sporolithon* sp. 1, and *Subterraniphyllum thomasii*. *Neogoniolithon* sp. 1, *Lithothamnion* sp. 2, *Mesophyllum* sp. 1 and *Polystrata alba* are also present. Thick encrustation sequences, including the encrusting foraminifera *Haddonia heissigi*, are especially common around coral fragments.

Corals totally dominate the rudstones with wacke-to packstone matrix of the coral facies and are often heavily encrusted. Coralline algae are subordinate with a slightly less diverse flora including common *Lithoporella melobesioides*, *Spongites* sp. 1 and sp. 2. *Neogoniolithon* sp. 1, *Lithothamnion* sp. 1, *Mesophyllum* sp. 1, *Sporolithon* sp. 1 and *Polystrata alba* also occur.

The grainstone facies is dominated by small, highly fragmented, highly abraded coralline algal remnants with subordinate miliolid foraminifera and corals. The coralline algal flora includes *Lithothamnion* sp. 2 and *Mesophyllum* sp. 1 as well as disarticulated intergenicula of geniculate coralline algae; *Spongites* sp. 2 is also present. The green algae *Cymopolia* sp. 1 and *Halimeda* sp. 1 are restricted to this facies.

The investigation of the calcareous algae is based on a detailed sampling of the Lower Oligocene Gornji Grad beds from a number of outcrops in the Gornji Grad area (Fig. 1). The calcareous algae were investigated using thin sections (5 x 5 cm and 10 x 8 cm). Anatomical and morphological terms used for the coralline red algae follow Woelkerling (1988, 1996), Woelkerling et al. (1993), and Braga et al. (1993). Measurements of cells and conceptacles were made by light microscopy; the orientation of cell and conceptacle dimensions follow Chamberlain et al. (1988). Anatomical and morphological terms used for the peyssonneliacean follow Bassi (1997), those for the dasycladacean follow De Castro (1997), and those for the halimedacean follow Bassoullet et al. (1983). All the specimens are deposited in the Institute and Museum of Geology and Palaeontology of the University of Tübingen (Germany).

Systematic comparisons.

The coralline algal species recognized at this stage of research in the Gornji Grad beds are named following an open nomenclature. The systematics study (see below) allowed the identification of 12 species belonging to 10 genera (Tab. 1): *Lithoporella melobesioides* (Foslie) Foslie 1909, *Neogoniolithon* sp. 1, *Spongites* sp. 1, *Spongites* sp. 2, *Lithothamnion* sp. 1, *Lithothamnion* sp. 2, *Mesophyllum* sp. 1, *Subterraniphyllum thomasii* Elliott 1957, *Sporolithon* sp. 1, *Polystrata alba* (Pfender) Denizot 1968 (Cryptonemiales, Peyssonneliaceae), *Halimeda* sp. 1 (Halimedaceae), and *Cymopolia* sp. 1 (Dasycladales, Dasycladaceae). Unidentified geniculate coralline algal fragments were also discovered.

According to the taxonomic concepts used by phycologists, the coralline red algal species recognized in the Gornji Grad beds shown similarities with some coralline species described in Upper Palaeogene successions of northern Italy, Austria, and Dalmatia. The difficulties faced when comparing fossil material to Recent coralline taxa or other fossil coralline algae have been outlined above. Comparisons were, nonetheless, made herein following the protologues and figured taxa in relevant original descriptions from the literature. In the current paper, these comparisons are usually limited to pointing out similarities to published accounts of other taxa without drawing definite taxonomic conclusions, unless fully justified by the data.

Lithoporella melobesioides is a species with a wide stratigraphical distribution. It has been identified in the

	protuberances			lamellae		encrusting	arborescent
	warty	lumpy	fruticose	layered	foliose		
Lithop. melobesioides						x	
Neogoniolithon sp. 1				x		x	
Spongites sp. 1	x					x	
Spongites sp. 2	x	x		o			
Lithothamnion sp. 1	x	x				x	
Lithothamnion sp. 2	o				x	x	
Mesophyllum sp. 1			x				
Geniculate corall. *s. l.*							x
Subterraniph. thomasii			x*				x*
Sporolithon sp. 1	x	x				o	
Polystrata alba				x	x	o	

Tab. 2 - Comparative summary of growth-forms (following Woelkerling et al., 1993), for each described species. Encrusting plants are entirely attached ventrally to the substratum; arborescent plants are tree-like with ramified branches. *Lithop.*= *Lithoporella*; *Subterraniph.*= *Subterraniphyllum*; corall. *s. l.* = corallines *sensu lato*; x = common; o = rare; * = the growth-form designation of *Subterraniphyllum* depends on its assignation as a geniculate (arborescent) or non-geniculate (fruticose) coralline algae (see text).

Middle Eocene of Austria (Rasser, 1994), in the Late Eocene of Veneto (Lake Garda and Colli Berici; Bassi, 1995 a, 1996, 1998), and in the Oligocene of Piedmont Basin (Mastrorilli, 1968 a).

Neogoniolithon sp. 1 is conspecific to *Mesophyllum* sp. 2 from the Upper Eocene Marne di Priabona of the Colli Berici, and to *Neogoniolithon* sp. 2 from the Upper Eocene Calcare di Nago of Lake Garda (Veneto; Bassi, 1995 a, 1998). This species also shows, however, close affinities with *Lithophyllum giammarini* Mastrorilli described by Francavilla et al. (1970) in the Colli Berici, with *Mesophyllum rigidum* Mastorilli and with *Lithophyllum contii* Mastrorilli from the Oligocene of the Piedmont Basin (Mastrorilli, 1968 a, c), and with *Lithophyllum pactum* Ishijima (1954) from the Miocene of Japan. *N.* sp. 1 also shows similarities with *N.* sp. described by Rasser & Piller (1999) from the Upper Eocene Austrian Molasse Zone.

Spongites sp. 1 shows similarities with *Lithophyllum vicetinum* Mastrorilli from the Middle-Late Eocene of Veneto (Mastrorilli, 1973).

Spongites sp. 2 compared with *Lithophyllum ligusticum* Airoldi (1932) and *L. pactum* Ishijima (1954).

Lithothamnion sp. 1 and *Lithothamnion* sp. 2 have vegetative affinities respectively with *L.* sp. 1 and *L.* sp. 2 described from the Late Eocene of northern Italy (Bassi, 1995 a, 1996). No fossil species described thus far show possible relationships with these species.

Mesophyllum sp. 1 is comparable to the homonym species in open nomenclature recorded in the Late Eocene of the Colli Berici and Lake Garda (Bassi, 1995 a, 1996, 1998). *Lithophyllum simplex* Lemoine and *L. symetricum* Lemoine described by Francavilla et al. (1970) can be compared with *M.* sp. 1.

Subterraniphyllum thomasii Elliott has so far been recognized in the Oligocene of the Middle East, Greece,

Borneo, Piedmont, Macedonia, and Colli Berici (see remarks in the Systematic palaeontology).

Sporolithon sp. 1 is compared to *S. aschersonii* (Schwager) Moussavian & Kuss (1990), but shows no similarities to it.

Polystrata alba has been identified from the Upper Cretaceous of Istria (Drobne et al., 1988, 1989), the Middle Eocene of Austria (Rasser, 1994), in Upper Eocene carbonate deposits outcropping in the eastern margin of Lake Garda (Calcare di Nago; Bassi, 1997, 1998), and to the Oligocene of the Piedmont Basin (Mastrorilli, 1968a).

Algal growth-forms.

The following growth-forms used for Recent coralline algae (Woelkerling et al., 1993) were recognized and applied to the fossil material: protuberances with warty (Pl. 1, fig. 1), lumpy (Pl. 1, fig. 2), and fruticose (Pl. 1, fig. 3) growth-forms; lamellae with layered (Pl. 1, fig. 4) and foliose (Pl. 1, fig. 4, 5) growth-forms; encrusting (Pl. 1, fig. 5); as well as arborescent (Pl. 1, fig. 8) growth-forms. Rhodoliths are not common in the studied limestones. In Tab. 2, a comparative summary of growth-forms for each described species is shown. *Spongites* sp. 2, *Lithothamnion* sp. 1 and sp. 2, *Sporolithon* sp. 1, and *Polystrata* alba have several different growth-form morphologies. *Spongites* sp. 2 shows growth-forms with protuberances or with lamellae. *Lithothamnion* sp. 1 and *Sporolithon* sp. 1 can develop as plants with protuberances or encrusting forms. *Lithothamnion* sp. 2 shows the highest diversity ranging from plants with protuberances, lamellae or encrusting thalli. The peyssonneliacean *Polystrata alba* usually occurs with a lamellate morphology, but can also grow as

an encrusting form. *Lithoporella melobesioides* was found only as encrusting thalli; *Mesophyllum* sp. 1 as fruticose plants. *Subterraniphyllum* is only present as fragments of branches. The geniculate corallines represent disarticulated fragments of arborescent plants. These results show a considerable variation in growth-forms at both the genus and species level.

Systematic Palaeontology

Division **Rhodophyta** Wettstein, 1901

Class R h o d o p h y c e a e Rabenhorst, 1863

Order C o r a l l i n a l e s Silva & Johansen, 1986

Family C o r a l l i n a c e a e Lamouroux, 1816

Subfamily M a s t o p h o r o i d e a e Setchell, 1943

Genus *Lithoporella* (Foslie) Foslie, 1909

Type species: *Lithoporella melobesioides* (Foslie) Foslie, 1909

Lithoporella melobesioides (Foslie) Foslie, 1909

Pl. 2, fig. 1

1968a *L. melobesioides* - Mastrorilli, p. 376-378, pl. 39, fig. 5.
1970 *L. melobesioides* - Vannucci, p. 472-474, pl. 9, fig. 1-2.
1994 *L. melobesioides* - Rasser, p. 198, pl. 3, fig. 3.
1995a *L. melobesioides* - Bassi, p. 91, pl. 1, fig. 8.
1996 *L. melobesioides* - Bassi, p. 149-150, pl. 22, fig. 1-6; pl. 23, fig. 1-4.
1998 *L. melobesioides* - Bassi, p. 19, pl. 7, fig. 4-6; pl. 8, fig. 1.

Morphology: Encrusting growth-forms, single or multiple overgrowths of cell filaments.

Vegetative anatomy: Dimerous plants with primigenous filaments with palisade cells 32-38 μm (M = 35, s.d. 3) high and 22-28 μm (M = 25, s.d. 3) in diameter. Postigenous filaments restricted to the fertile portions of the plants. Cell fusions present.

Rare tetra/bisporangial uniporate conceptacles are very poorly preserved. No measurements were taken.

Remarks: The thin dimerous thallus with large cells (i.e. 10-35 μm high and 25-70 μm in diameter, from present-day material in Woelkerling, 1996, p. 253), the presence of cell fusions, and the tetra/bisporangial uni-

porate conceptacles ascribed the specimens to the genus *Lithoporella* (Woelkerling, 1988; Braga et al., 1993). *L. melobesioides* has been identified both in fossil and in Recent material (Woelkerling, 1988). This species has been recorded in the Oligocene of the Piedmont Basin (Mastrorilli, 1968a), in the Middle Eocene of Austria (Rasser, 1994), in the Late Eocene both of eastern Lake Garda and Colli Berici (northern Italy; Bassi, 1995 a, 1996, 1998). This species is present in the coralline algal, coralline algal-coral, and coral facies and usually occurs as thin crusts around corals, larger foraminifera, and other algae.

Genus *Neogoniolithon* Setchell & Mason, 1943

Lectotype species: *Neogoniolithon fosliei* (Heydrich) Setchell & Mason 1943, designed by Penrose (1992)

Neogoniolithon sp. 1

Pl. 2, fig. 2-8

1995a *Mesophyllum* sp. 2 - Bassi, p. 90, pl. 1, fig. 5-6; text-fig. 8 B.
1998 *Neogoniolithon* sp. 2 - Bassi, p. 18, pl. 6, fig. 2-6.

Morphology: Encrusting and layered growth-forms, with thallus thickness up to 500 μm.

Vegetative anatomy: Monomerous coaxial thallus; core filaments with cells 21-29 μm (M = 25, s.d. 4) long and 12-16 μm (M = 14, s.d. 2) in diameter; cell of adjacent filaments connected laterally by cell fusions. Peripheral filaments bending away from core region and gradually becoming oriented perpendicularly to thallus surface; cells 15-21 μm (M = 18, s.d. 3) long and 12-20 μm (M = 16, s.d. 4) in diameter; cell fusions connecting the contiguous filaments. Epithallial cells not seen.

Tetra/bisporangial uniporate conceptacles sub-triangular in shape, rise above the thallus surface; conceptacle chambers 262-286 μm (M = 274, s.d. 12) long and 677-693 μm (M = 685, s.d. 8) in diameter and lacking a central columella. Conceptacle roof protruding conspicuously above surrounding thallus surface, formed by filaments peripheral to fertile areas; depth of the tetra/bisporangial conceptacle floor of 10-17 cells; pore canal conical in shape, 6-7 cell filaments high, lined by cells

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PLATE 1

Scale bars: 1 mm for Fig. 7, 8; 2 mm for Fig. 1, 2, 4, 6; 4 mm for Fig. 3; 6 mm for Fig. 5.

Fig. 1   - Warty (verrucose) protuberances of *Sporolithon* sp. 1, DU1.20.
Fig. 2   - Lumpy protuberances of *Lithothamnion* sp. 2 and *Neogoniolithon* sp. 1 (upper left corner), KB5.1.
Fig. 3   - Fruticose protuberances of *Lithothamnion* sp. 1, SLO94-020.
Fig. 4   - Layered to foliose plants of *Lithothamnion* sp. 2, DU1.20.
Fig. 5   - Foliose (lamellae) to encrusting plants of *Polystrata alba* and *Sporolithon* sp. 1, KO15.
Fig. 6   - Bifurcating layered to foliose crusts of *Neogoniolithon* sp. 1, DU3.16.
Fig. 7   - Fragments of branches of arborescent geniculate corallines s.l., SLO94-044.
Fig. 8   - Arborescent tree-like algal fragment of *Mesophyllum* sp. 1, DU3.42.

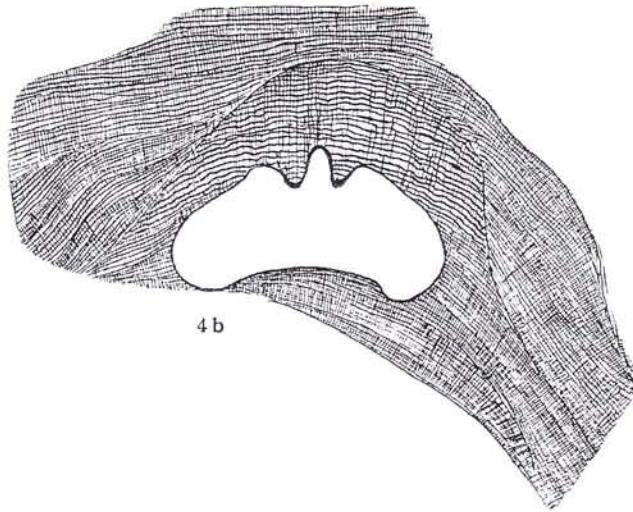Pl. 1   Calcareous algae from the Lower Oligocene of Slovenia   105
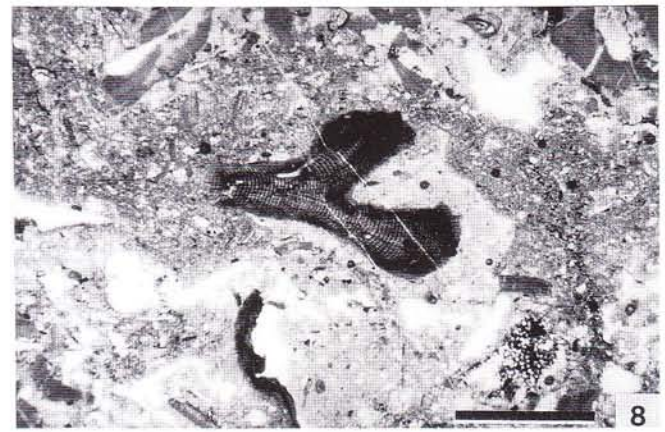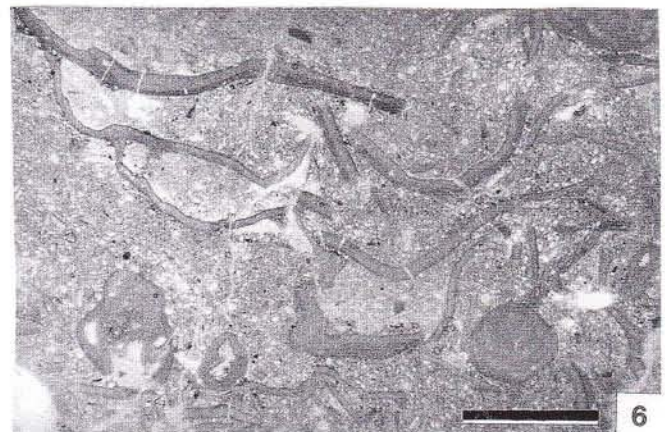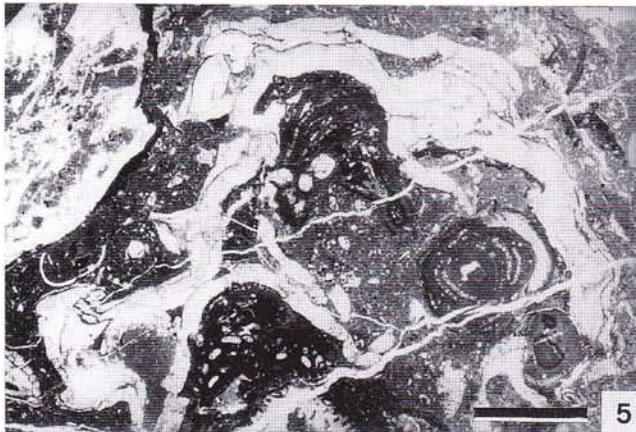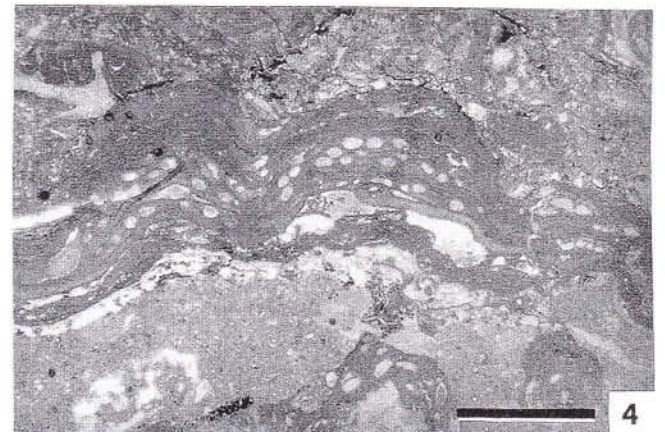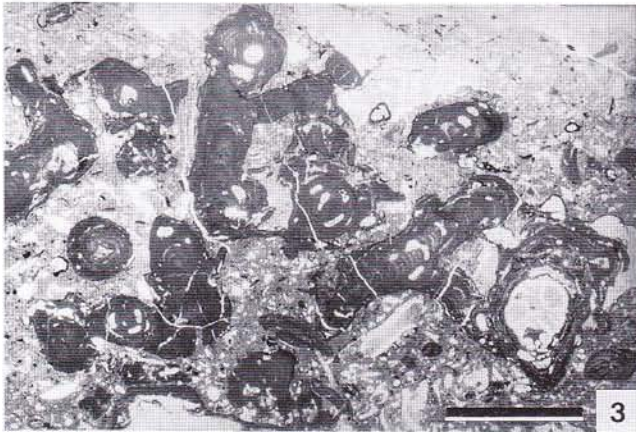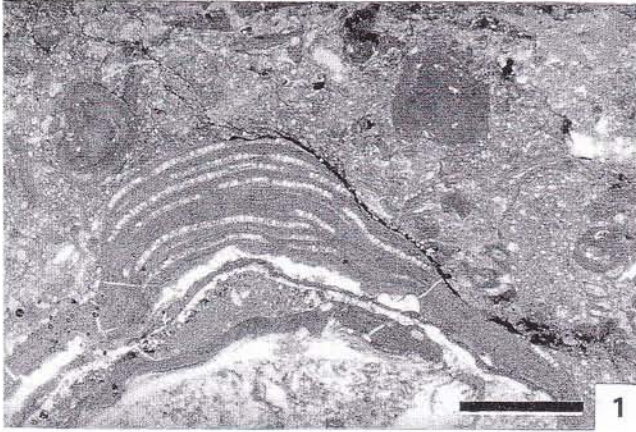
Fig. 2 - Original fig. 4 b (*Lithophyllum pactum* Ishijima, holotype; X 50) in Ishijima (1954, pl. 26) showing a drawing of an uniporate conceptacle.

oriented more or less parallel to thallus surface and protruding laterally into the canal.

Remarks: The monomerous coaxial core filaments with cell fusions, secondary pit-connections absent, the tetra/bisporangial uniporate conceptacles, pore canal of the conceptacles bordered by cell filaments subparallel to the roof and protruding into the canal allow the identification of the genus *Neogoniolithon* (Woelkerling, 1988, 1996; Braga et al., 1993). These features also are found in *Spongites* Kützing and in *Pneophyllum* Kützing (i.e. Penrose, 1996; Woelkerling, 1996). These genera are separated from one another on the basis of the arrangement of cell filaments around the pore canals and on the basis of the gonimoblast filaments (Woelkerling, 1996, p. 238; Penrose & Woelkerling, 1991). In particular, for the *Neogoniolithon* circumscription, Penrose (1992) and Penrose & Chamberlain (1993) consider features related to reproductive cells (i.e. gonimoblast filaments) which, so far are only known in Recent material (see also Rasser & Piller, 1999).

Neogoniolithon sp. 1 is conspecific to *Mesophyllum* sp. 2 (Bassi, 1995a) and *N.* sp. 2 (Bassi, 1998) identified in the Late Eocene of northeastern Italy. *M.* sp. 2 has been found within the Upper Eocene Marne di Priabona (Colli Berici) and *N.* sp. 2 in the Calcare di Nago (eastern Lake Garda). Bassi (1995a), by comparing *M.* sp. 2 to *Mesophyllum* cf. *rigidum* and *Lithophyllum giammarini* described by Francavilla et al. (1970), concluded that these two latter species could be included within *Mesophyllum* sp. 2. Mastrorilli's (1968a) assignment of the species "*rigidum*" to the genus *Mesophyllum* may be untenable. The subfamily Melobesioideae, to which *Mesophyllum* belongs, is characterised by the presence of multiporate tetra/bisporangial conceptacles and uniporate gametangial conceptacles (Woelkerling, 1988, 1996; Braga et al., 1993). The protologue of *Mesophyllum rigidum* Mastrorilli (Mastrorilli, 1968a) does not describe any multiporate conceptacles. Moreover, Mastrorilli's illustration (pl. 18, fig. 3) shows an oblique non-axial section of one conceptacle which closely resembles a uniporate conceptacle rather than a multiporate one. Such a uniporate conceptacle might be a gametangial conceptacle. Without some evidence of what the conceptacle contained, it is impossible to determine whether it belongs to a melobesioid genus or not.

Francavilla et al.'s (1970) illustrations of *M.* cf. *rigidum* (pl. 85, fig. 2, 3) do not show any conceptacle. This, along with the descriptions of the vegetative characters and the illustrations reported by Mastrorilli (1968a) and Francavilla et al. (1970), suggests that the species "*rigidum*" be assigned to the genus *Neogoniolithon* rather than to *Mesophyllum*.

Lithophyllum giammarini described by Francavilla et al. (1970) (see revision of *L. contii* Mastrorilli *sensu amplo* made by Fravega & Vannucci, 1987b) clearly shows a uniporate conceptacle (pl. 86, fig. 1, 2) which resembles that described herein for *Neogoniolithon* sp. 1; furthermore, Francavilla et al. (1970, pl. 86, fig. 1) show a monomerous coaxial thallus with cell fusions. There is, therefore, no firm evidence at present that would exclude *Mesophyllum rigidum* Mastrorilli and *Lithophyllum contii* Mastrorilli s.a. from the genus *Neogoniolithon* (subfamily Mastophoroideae).

Neogoniolithon sp. 1 described here may be also compared to *Lithophyllum pactum* Ishijima (1954) which shows similar vegetative features (Ishijima, 1954, p. 44)

PLATE 2

Fig. 1 - *Lithoporella melobesioides* (Foslie) Foslie, multiple overgrowths of dimerous cell filaments, SLO94-043; scale bar= 200 μm.

Fig. 2 - *Neogoniolithon* sp. 1, crust showing coaxial cell arrangement of the monomerous thallus, KB4.4; scale bar= 1 mm.

Fig. 3 - *Neogoniolithon* sp. 1, section through a monomerous thallus showing the central coaxial core filament and the cell fusions, SLO94-041; scale bar= 100 μm.

Fig. 4 - *Neogoniolithon* sp. 1, transversal section of the thick monomerous thallus showing a tetra/bisporangial uniporate conceptacle raising above the thallus surface, SLO94-004; scale bar= 50 μm.

Fig. 5 - *Neogoniolithon* sp. 1, uniporate conceptacle showing the cell filaments oriented more or less parallel to the outer conceptacle roof, KB5.1; scale bar= 150 μm.

Fig. 6 - *Neogoniolithon* sp. 1, longitudinal section of the thick monomerous thallus showing a tetra/bisporangial uniporate conceptacle, KB4.3; scale bar= 50 μm.

Fig. 7, 8 - *Neogoniolithon* sp. 1, details of tetra/bisporangial uniporate conceptacles, KB6.1; scale bar= 30 μm.
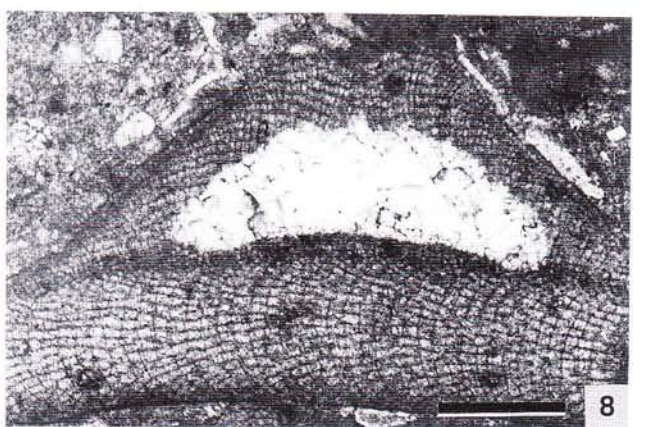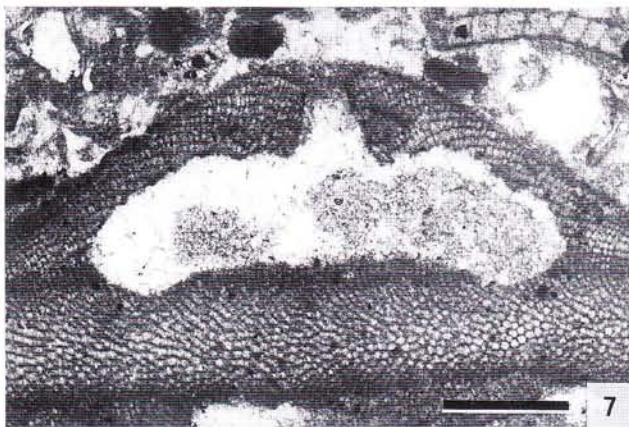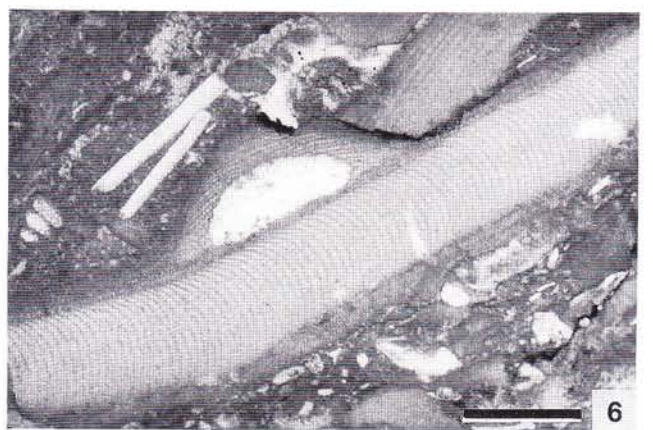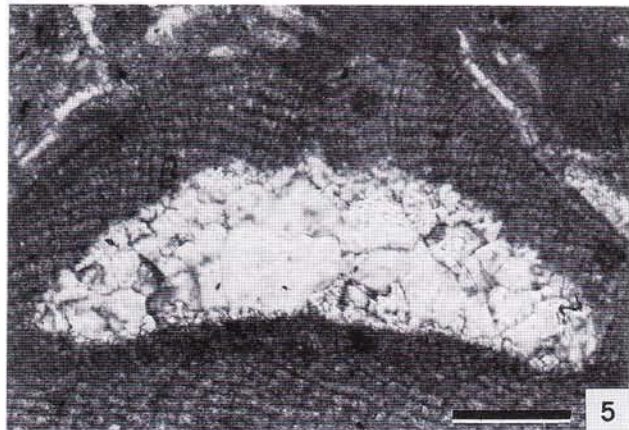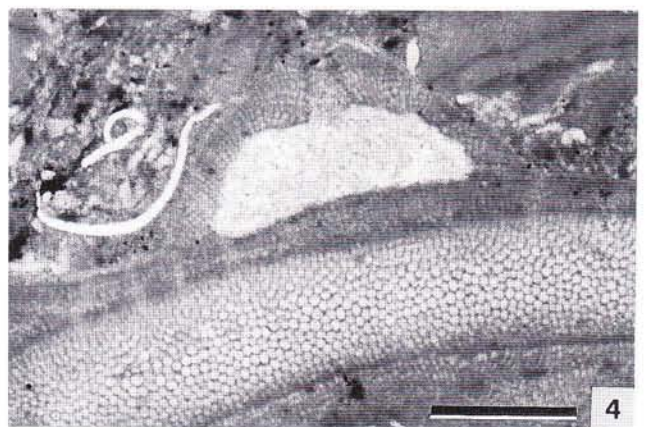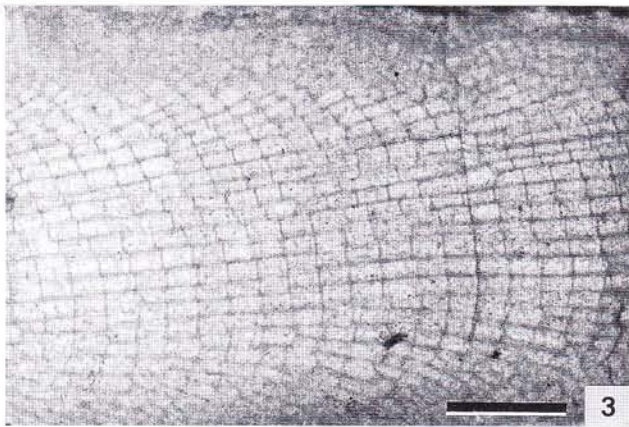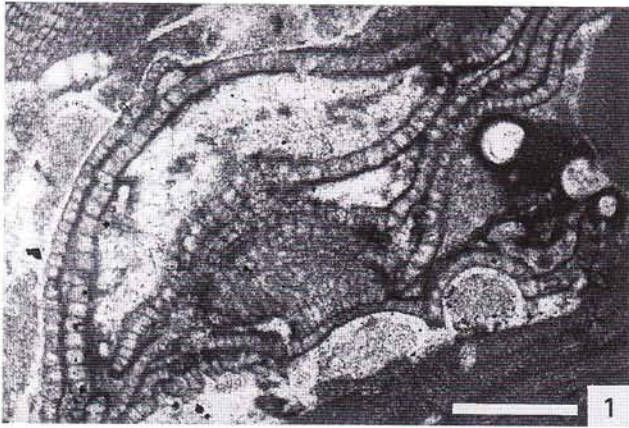
as well as conceptacle shape and size (Ishijima, 1954, pl. 26, fig. 4a-b, 5; Fig. 2). Furthermore, *Neogoniolithon* sp. 1 shows similarities with *Neogoniolithon* sp. described by Rasser & Piller (1999) from the Upper Eocene Austrian Molasse Zone. *N.* sp. 1 differs from *N.* sp. (Rasser & Piller, 1999) in having an arcuate conceptacle chamber floor and shorter pore canals.

Neogoniolithon sp. 1 characterises the coralline algal facies and is uncommon in the coralline algal-coral and coral facies. Samples measured: KB1.1, KB4.3, KB4.1.

Genus *Spongites* Kützing, 1841

Lectotype species: *Spongites fruticulosus* Kützing, 1841 designated by Woelkerling (1985)

Spongites sp. 1
Pl. 3, fig. 1-4

Morphology: Plants encrusting or warty with unbranched protuberances mostly less than 1.0 mm height.

Vegetative anatomy: Thallus arrangement monomerous; ventral filaments, with cells 12-17 μm (M = 14.5, s.d. 2.5) long and 10-14 μm (M = 12, s.d. 2) in diameter, curve upwards into the peripheral region. This is formed by rectangular cells 13-20 μm (M = 16.5, s.d. 3.5) long and 11.5-21.5 μm (M = 16.5, s.d. 5) in diameter; cell fusions connect contiguous filaments. Epithallial cells not preserved.

Tetra/bisporangial, uniporate conceptacles with conical pore canal; chambers are bean-shaped in section, 83-95 μm (M = 89, s.d. 6) high and 299-313 μm (M = 306, s.d. 7) in diameter; depth of tetra/bisporangial conceptacle chamber floor of 6-7 cells; central columella about 30 μm high. Pore canal 101-105 μm (M = 103, s.d. 2) long and 33-37 μm (M = 35, s.d. 2) in diameter, lined by numerous small cells arranged in 10-11 filaments subparallel to the roof surface. The conceptacles are buried within the thallus.

Remarks: The monomerous construction, the presence of cell fusions, tetra/bisporangial uniporate conceptacles, and pore canal of the conceptacles bor-

dered by cell filaments subparallel to the roof and protruding into the canal, as well as the absence of secondary pit-connections allow the genus *Spongites* to be identified (Woelkerling, 1988, 1996; Penrose & Woelkerling, 1992; Braga et al., 1993). This species encrusts corals in the coralline algal-coral and coral facies and is present in the coralline algal facies. Samples measured: SLO94-027B, SLO94-O21A, SLO94-004, SLO94-003A, D 3.64, KB4.4, KO16.

Hydrolithon may differ from *Spongites* in possessing tetra/bisporangial conceptacle pore canals lined by cells that are orientated more or less perpendicularly to the roof surface (e.g. Woelkerling, 1985; Woelkerling, 1996, p. 238), and from *Neogoniolithon* in the latter having tetra/bisporangial conceptacle roof formed only by filaments peripheral to the sporangial initials (Woelkerling, 1996). Furthermore, *Spongites* differs from *Lithophyllum* in having fusions between cell filaments and lacking secondary pits (i.e. Woelkerling, 1988, 1996; Braga et al., 1993). In most identification keys of fossil corallines, the recognition of uniporate conceptacles and non-coaxial core filaments ("plumose" arrangement) defines *Leptolithophyllum* and *Tenarea* (Conti, 1950, p. 95-96; Poignant, 1979, p. 759-760), and sometimes *Lithophyllum* (Lemoine, 1939, p. 37-39). According to Woelkerling (1988), *Leptolithophyllum* is not recognized as a valid taxon (p. 103-104), and *Tenarea* and *Lithophyllum* which both lack cell fusions belong to the subfamily Lithophylloideae.

Spongites sp. 1 shows similarities with *Lithophyllum vicetinum* Mastrorilli (1973) as far as the conceptacle size and the occurrence of cell fusions is concerned (see Mastrorilli, 1973, pl. 6, fig. 3). A rigorous revision of the *L. vicetinum* type material is needed with respect to the diagnostic characters of families and subfamilies of present-day Lithophylloideae (neontological approach; Braga & Aguirre, 1995; Woelkerling, 1996).

Spongites sp. 2
Pl. 3, fig. 5-8

Morphology: Warty, lumpy, and rarely layered growth-forms. The protuberances are usually up to 1.5 mm long and 2.0 mm in diameter.

PLATE 3

Fig. 1 - *Spongites* sp. 1, uniporate conceptacle showing the cylindrical pore canal bordered by cells (arrow) that protrude into the canal and are oriented more or less parallel to the roof surface, SLO94-021; scale bar= 130 μm.

Fig. 2, 3 - *Spongites* sp. 1, uniporate pore canal lined by numerous small cells arranged in filaments subparallel to the roof surface and protruding into the canal (arrow), KB4.4; scale bar= 200 μm.

Fig. 4 - *Spongites* sp. 1, detail of the conceptacle wall cell filaments, SLO94-021; scale bar= 80 μm.

Fig. 5 - *Spongites* sp. 2, high protuberance showing distinct growth-rhythms and conceptacles, KB4.4; scale bar= 50 μm.

Fig. 6 - *Spongites* sp. 2, details of the uniporate conceptacle roof, KB2.3; scale bar= 160 μm.

Fig. 7 - *Spongites* sp. 2, several sections of uniporate conceptacles showing the pore canal cylindrical in shape, DU3.42; scale bar= 200 μm.

Fig. 8 - *Spongites* sp. 2, non-coaxial core filaments (c) and conceptacle cell wall, KO-015; scale bar= 200 μm.
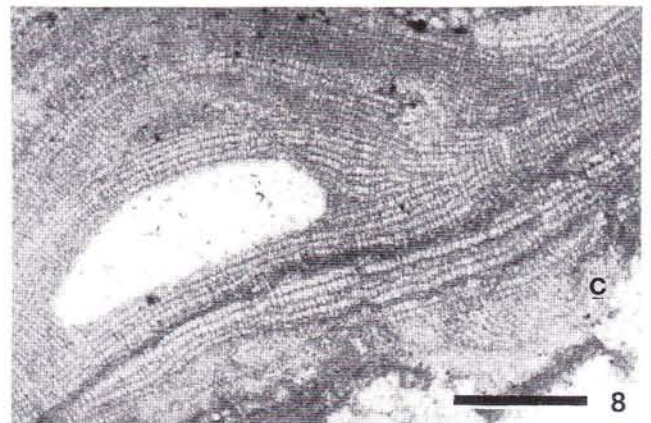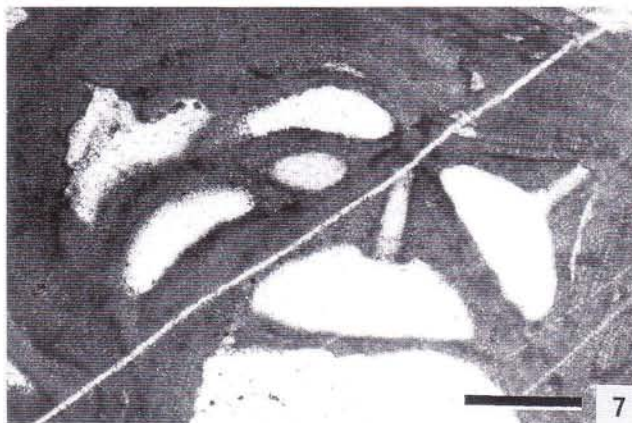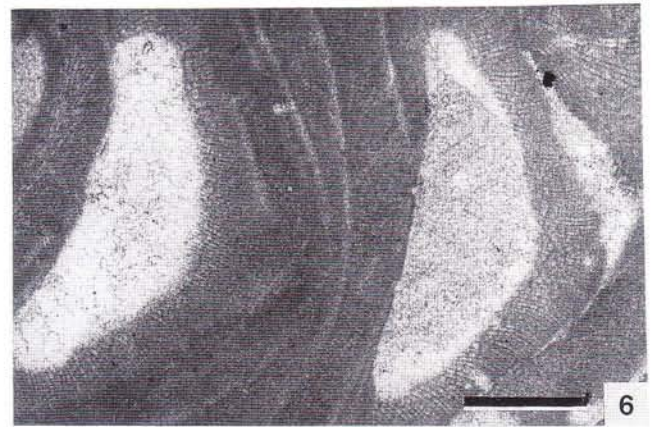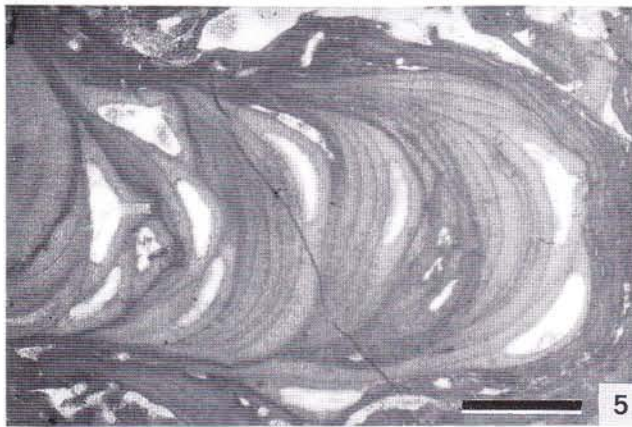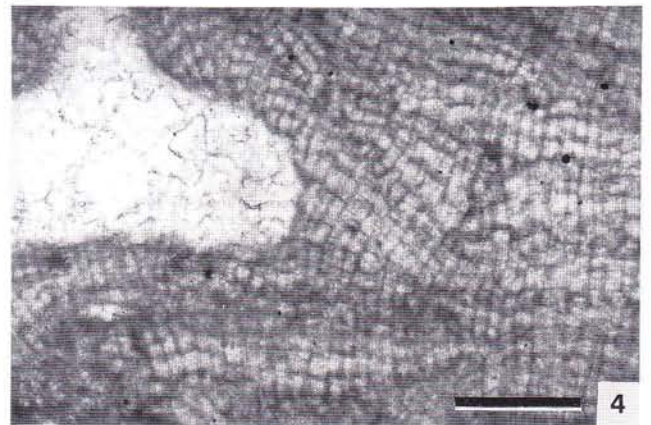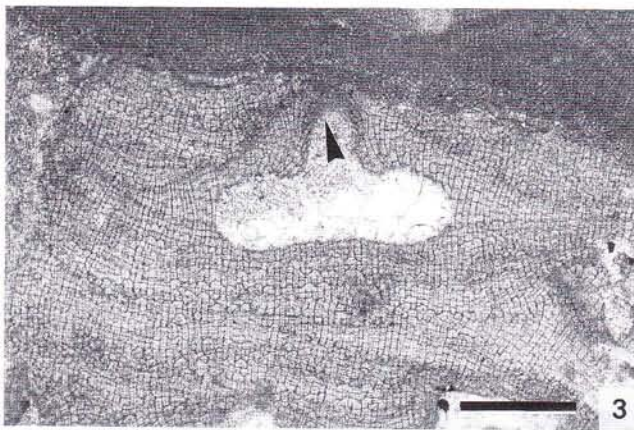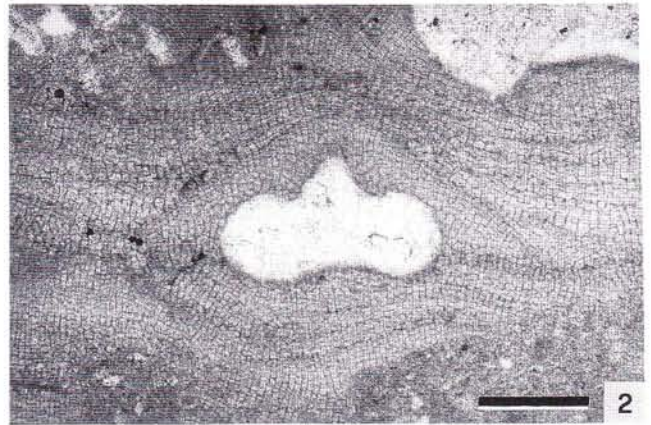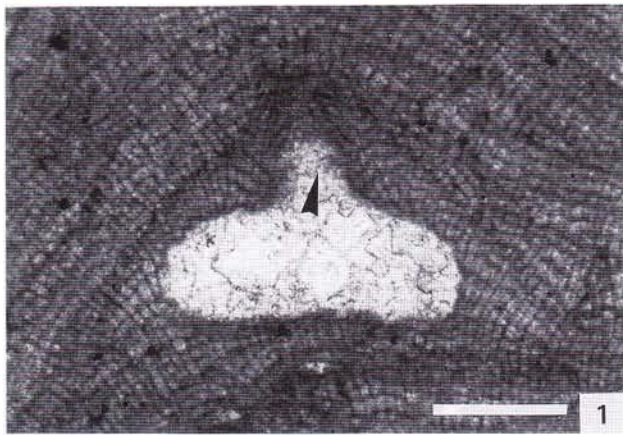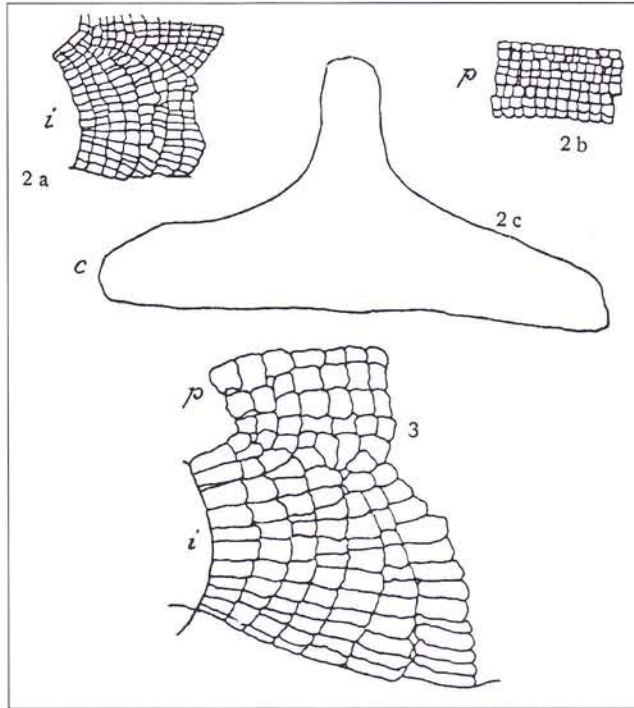
Fig. 3   - Original fig. 2 a-c (X 155) and fig. 3 (X 325) in Airoldi (1932, pl. 3), holotype of *Lithophyllum ligusticum* Airoldi; 'i' and 'p' denote the 'hypothallium' and 'perithallium', 'c' the conceptacle.

Vegetative anatomy: Thallus arrangement monomerous; core filaments non-coaxial with cells 13-17 μm (M = 15, s.d. 2) long and 7-9 μm (M = 8, s.d. 1) in diameter. Postigenous filaments contain cells 16-20 μm (M = 18, s.d. 2) long and 8-10 μm (M = 9, s.d. 1) in diameter; cell fusions occurring between cells of contiguous filaments. Subepithallial and epithallial cells not found.

Tetra/bisporangial uniporate conceptacles flask-like to triangular in shape; conceptacle roof protruding above surrounding thallus surface; chambers 155-165 μm (M = 160, s.d. 5) high and 469-481 μm (M = 475, s.d. 6) in diameter. Pore canal cylindrical in shape, 171-175 μm (M = 173, s.d. 2) high and 40-48 μm (M = 44, s.d. 4) in diameter at the base; depth of tetra/bisporangial conceptacle chamber floor of 6-9 cells; no columella found.

Remarks: The following combination of characters distinguish *S.* sp. 2 from *S.* sp. 1: a) larger tetra/bisporangial conceptacles; b) conceptacles flask to triangular in shape; c) conceptacles rise above the thallus surface. This species shows warty, lumpy growth-forms and rarely layered fragments. It is common in the coralline algal, coralline algal - coral and coral facies and is present in the grainstone facies. Samples measured: SLO94-019, KB2.3, KO15, DU1.21, DU3.42.

Spongites sp. 2 shows similarities to *Lithophyllum ligusticum* Airoldi (1932), described from the Oligocene of the Piedmont Basin. Airoldi (1932) identified *Lithophyllum* on the base of uniporate conceptacles and the non-coaxial cell filaments of the "hypothallium" (Fig. 3). According to the original protologue (Airoldi, 1932, p. 72-73) and other records (Beckmann & Beckmann, 1966, pl. 4, fig. 46, 47; Mastrorilli, 1968a, pl. 22, fig. 1-3; Vannucci, 1970, pl. 5, fig. 4; Stockar, 1997, fig. 14, 15), the conceptacle size ranges from 110-200 μm (max 290 μm) high to 430-550 μm in diameter. *L. ligusticum* has a longer pore canal than *S.* sp. 2 described here; the characters related to the pore canal and the chamber floor are not mentioned in the protologue (Airoldi, 1932, p. 72-73). Furthermore, *Spongites* sp. 2 described here may be also compared to *Lithophyllum pactum* Ishijma recognized by Vannucci (1970; pl. 6, fig. 2, 3) which shows similar conceptacle and pore canal shapes and sizes as well as vegetative features.

Subfamily Melobesioideae Bizzozero, 1885
Genus *Lithothamnion* Heydrich, 1897

Lectotype species. *Lithothamnion muelleri* Lenormand ex Rosanoff, 1866 designated by Woelkerling (1983)

Lithothamnion sp. 1
Pl. 4, fig. 1-3

Morphology: Growth-forms vary from warty to lumpy to encrusting, with protuberances reaching up to 3 mm long and 1-2.5 mm wide.

PLATE 4

Fig. 1   - *Lithothamnion* sp. 1, fertile protuberance bearing multipored tetra-bisporangial conceptacles with sterile filaments, DU1.22; scale bar= 1 mm.

Fig. 2, 3 - *Lithothamnion* sp. 1., section through multiporate conceptacle showing roof structure, DU3.42, KB4.1; scale bar= 200 μm.

Fig. 4   - *Lithothamnion* sp. 2, fertile protuberances and uniporate conceptacles-bearing coaxial thalli of *Neogoniolithon* sp. 1 (arrow), KB5.2; scale bar= 1 mm.

Fig. 5   - *Lithothamnion* sp. 2, distinct growth-rhythms and multiporate conceptacles, SLO94-043; scale bar= 50 μm.

Fig. 6   - *Lithothamnion* sp. 2, superimposed growths with multiporate conceptacles, DU3.42; scale bar= 160 μm.

Fig. 7   - *Lithothamnion* sp. 2, protuberance with distinct growth-rhythms and several conceptacles showing sterile filaments, SLO94-037; scale bar= 200 μm.

Fig. 8   - *Lithothamnion* sp. 2, section through tetrasporangial conceptacles showing sterile filaments and roof structure, DU3.42; scale bar= 200 μm.
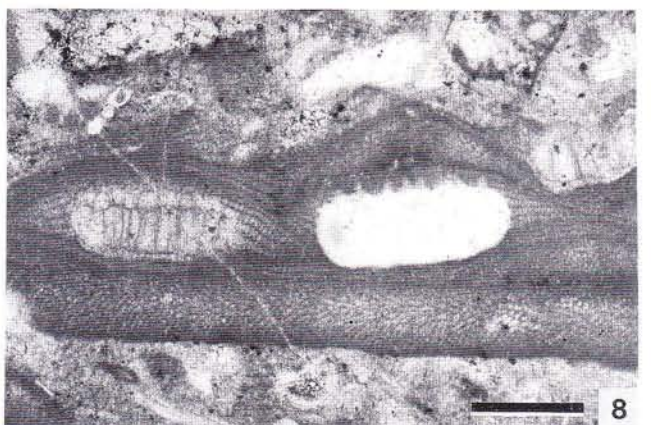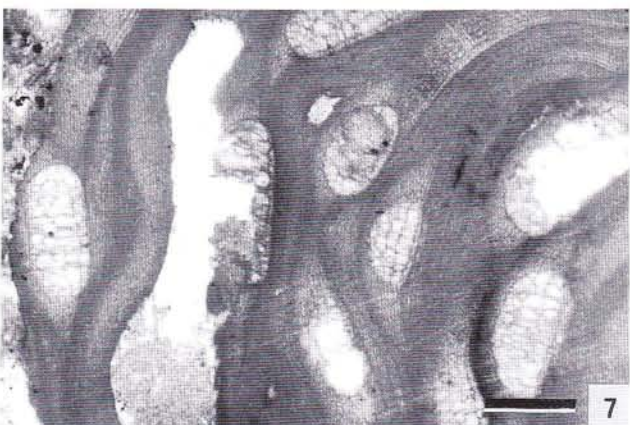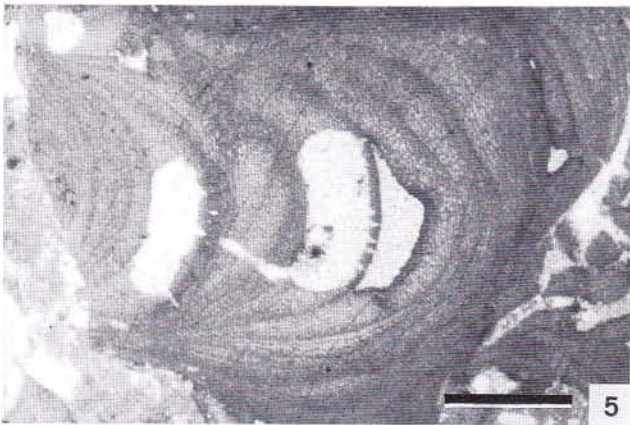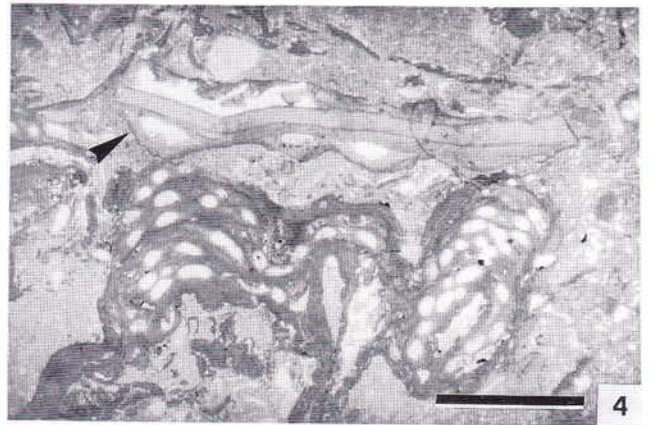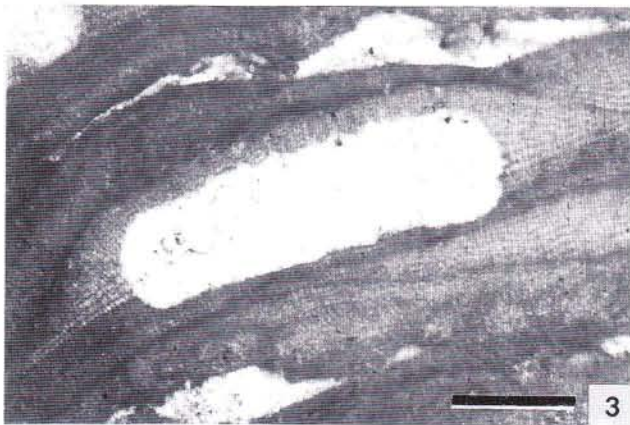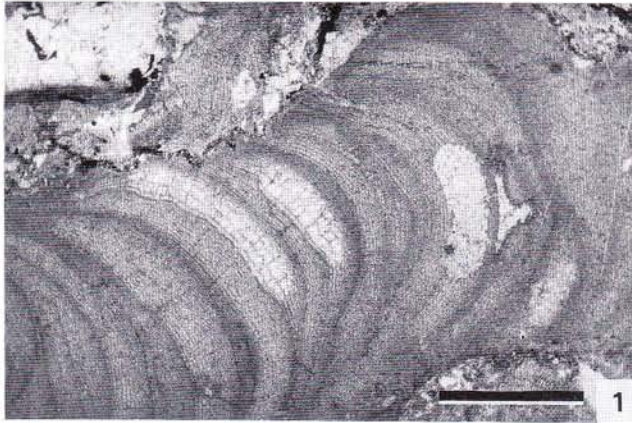
Pl. 4   *Calcareous algae from the Lower Oligocene of Slovenia*   111

Vegetative anatomy: Dorsiventral cell filament organisation in crustose portions and radial in protuberances; core filaments non-coaxial, core portion about 48 µm thick; cells 10-14 µm (M = 12, s.d. 2) long and 7-9 µm (M = 8, s.d. 1) in diameter; core filaments curve outwards towards the thallus surface. Peripheral region with cells 14-20 µm (M = 17, s.d. 3) long and 8-10 µm (M = 9, s.d. 1) in diameter. Cells of adjacent filaments connected laterally by fusions. Rare flat epithallial cells.

Tetra/bisporangial conceptacles multiporate; conceptacle chamber 584-596 µm (M = 590, s.d. 6) in diameter and 176-184 µm (M = 180, s.d. 4) high; conceptacle roof protruding above or flush with surrounding thallus surface, 51-57 µm (M = 54, s.d. 3) thick, and composed of 5-7 cell layers, with cells 8 µm long and 8 µm in diameter; depth of tetra/bisporangial conceptacle chamber floor of about 15 cells. Pores diameter of 11-13 µm (M = 12, s.d. 1). Conceptacles are buried within the thallus.

Remarks: The monomerous non-coaxial thallus with cell fusions and the multiporate tetra/bisporangial conceptacles are distinctive features of the melobesioid genera *Lithothamnion* Heydrich 1897, *Clathromorphum* Foslie 1898, and *Phymatolithon* Foslie 1898 (Woelkerling, 1988; Braga et al., 1993; Wilks & Woelkerling, 1995). The main characters used to differentiate these genera are the relative size and the shape of the epithallial cells, which can be flat but not flared in the last two genera. The specimens described here show rare flat epithallial cells suggesting the taxon *Lithothamnion*. However, a rigorous identification at genus level was not possible and further studies (also by SEM) on epithallial cell shape are needed.

L. sp. 1 shows vegetative affinities with *L.* sp. 1 described from the Late Eocene of northern Italy (Bassi, 1995a, 1996). This species is common in the foraminiferal-coralline algal, coralline algal, coralline algal-coral facies and is present in the coral facies mostly as warty growth-forms. Samples measured: KB4.1, KB4.3, DU3.42A. No fossil species described up to now show comparable characters with *L.* sp. 1.

Lithothamnion sp. 2

Pl. 4, fig. 4-8

Morphology: Plants encrusting to foliose; rarely warty growth-forms with 1 mm long and less than 1 mm wide protuberances.

Vegetative anatomy: Dorsiventral cell filament organisation in crustose portions and radial in protuberances; core filaments non-coaxial, core portion 50-155 µm thick; in the foliose portions it reaches up to the 50% of the thallus; cells 15-21 µm (M = 18, s.d. 3) long and 8-12 µm (M = 10, s.d. 2) in diameter; core filaments curve outwards towards the thallus surface. Peripheral region with cells 11-13 µm (M = 12, s.d. 1) long and 7-9 µm (M = 8, s.d. 1) in diameter. Cells of adjacent filaments connected laterally by fusions. Rare flat epithallial cells.

Tetra/bisporangial conceptacles multiporate; conceptacle roof rising above thallus surface, 32-38 µm (M = 35, s.d. 3) thick, composed of 4-6 cell layers with cells 10 µm long and 8 µm in diameter; conceptacle chamber 337-343 µm (M = 340, s.d. 3) in diameter and 130-140 µm (M = 135, s.d. 5) high. Pore canals are 10-12 µm in diameter and are lined by filaments whose cells do not differ markedly from those of the surrounding roof. Conceptacles preserved at different aborted stages of development are very common. Mature conceptacles may coexist with conceptacles fossilised when decalcified structures were developing (Pl. 4, Fig. 7-8).

Remarks: *L.* sp. 2 differs from *L.* sp. 1 in conceptacle size, rising of conceptacle roofs, and number of conceptacle roof cell filaments. *L.* sp. 2 shows characteristics of the species *L.* sp. 2 described and illustrated from the Upper Eocene Marne di Priabona of the Colli Berici (Bassi, 1995 a, 1998). This latter species, however, has larger multiporate conceptacles and no conceptacle roof features have been reported. This species is common in the grainstone facies and is present in the coralline algal and coralline algal-coral facies. Samples measured: KB4.3, KB5.2, KO16, DU3.16, DU3.22, DU3.42, DU3.47, DU3.55, DU3.57. No fossil species described thus far show similarities to *L.* sp. 1.

Genus *Mesophyllum* Lemoine, 1928

Lectotype species: *Mesophyllum lichenoides* (Ellis) Lemoine, 1928 designated by Ishijima (1942)

Mesophyllum sp. 1

Pl. 5, fig. 1-3

1995a *Mesophyllum* sp. 1 - Bassi, p. 88-90, pl. 1 fig. 4; text-fig. 8A.
1998 *Mesophyllum* sp. 1 - Bassi, p. 15-16, pl. 3, fig. 1-3.

PLATE 5

Fig. 1   - *Mesophyllum* sp. 2, multiporate conceptacles strongly rising from the thallus surface, SLO94-043; scale bar= 200 µm.
Fig. 2, 3 - *Mesophyllum* sp. 2, longitudinal sections of a single branch showing coaxial cell arrangements in adjacent core filaments, SLO94-043; scale bar= 100 µm; scale bar= 500 µm.
Fig. 4   - Geniculate coralline *s.l.*, SLO94-044; scale bar= 50 µm.
Fig. 5, 6 - Geniculate coralline *s.l.*, KB5; scale bar= 50 µm; SLO94-038, scale bar= 1 mm.
Fig. 7   - *Subterraniphyllum thomasii* Elliott, microfacies, St.A.94-044; scale bar= 1 mm.
Fig. 8   - *Subterraniphyllum thomasii* Elliott, oblique transverse section through a dichotomous branch, St.A.94-044; scale bar= 500 µm.
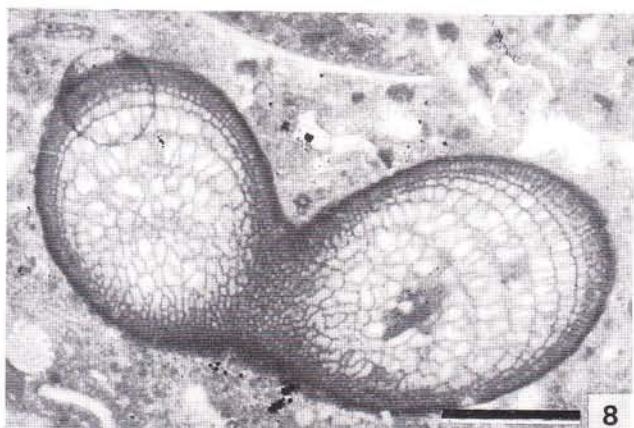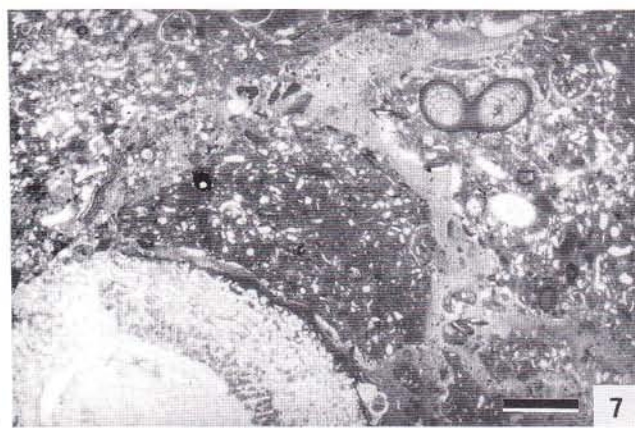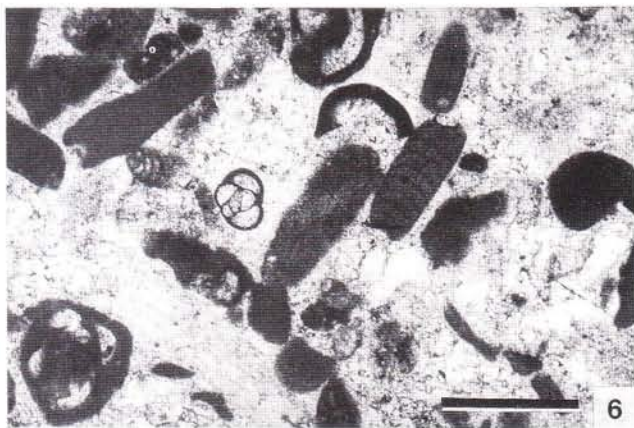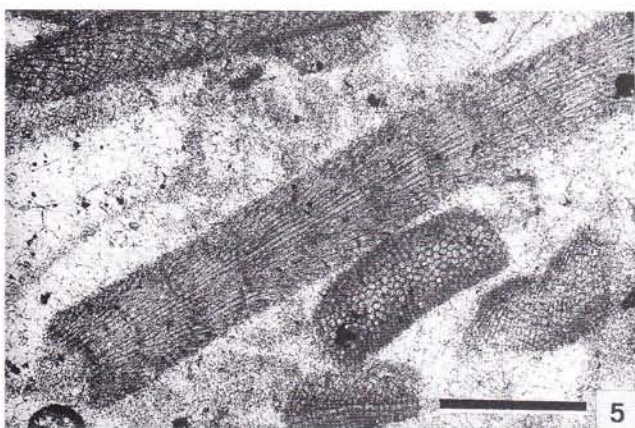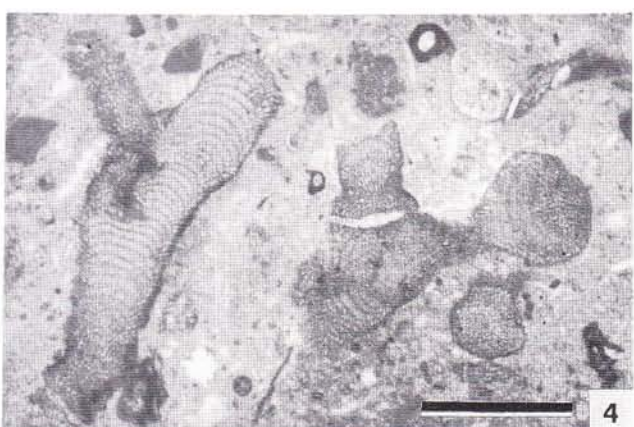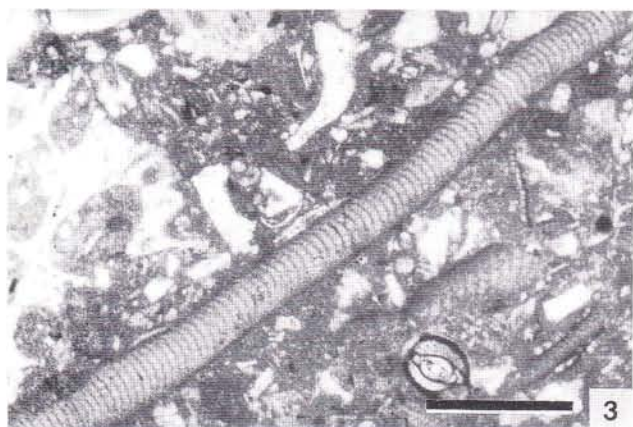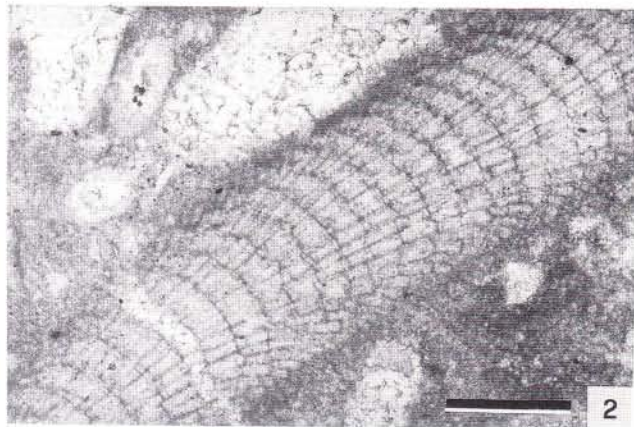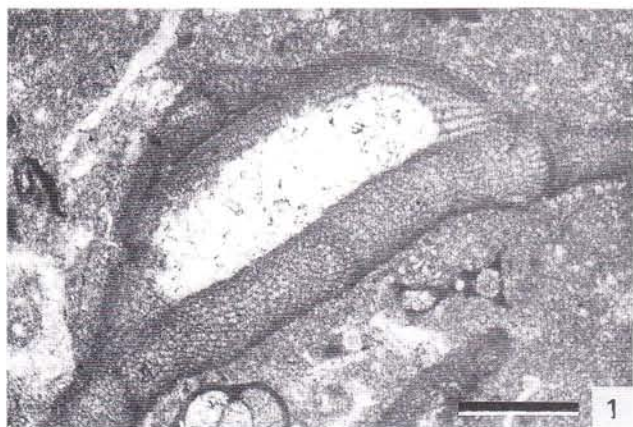
Fig. 4.

Fig. 5.

Fig. 4 - Original fig. 4 (*Lithophyllum simplex* Lemoine, holotype) and fig. 5 (*Lithophyllum symetricum* Lemoine, holotype) in Lemoine (1927, p. 549). No conceptacle was represented.

Morphology: Fruticose plants with branches mostly 250 μm in diameter.

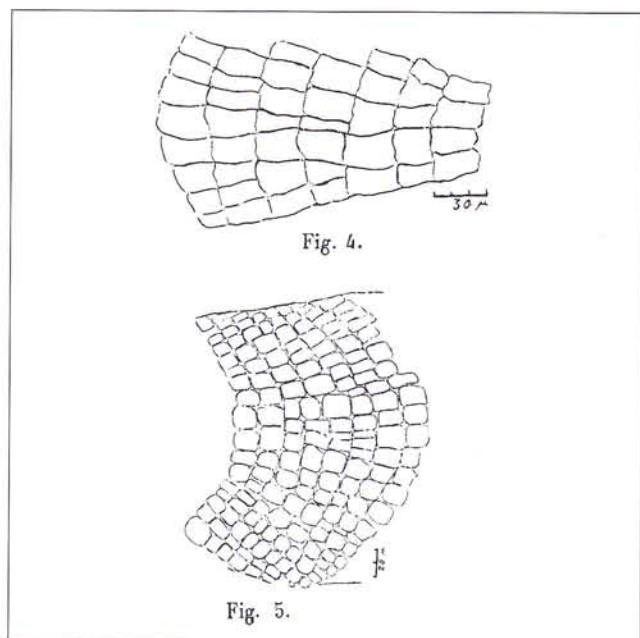**Vegetative anatomy**: Thallus monomerous; internal organisation radial, composed of a single system of cell filaments that form a central coaxial core with arching tiers of cells when viewed in longitudinal section; cells 21-27 μm (M = 24, s.d. 3) long and 12-16 μm (M = 14, s.d. 2) in diameter in core region. No epithallial cells have been recognized. Cells of adjacent filaments connected by cell fusions.

Tetra/bisporangial multiporate conceptacles rising strongly above the thallus surface; conceptacle chambers 482-518 μm (M = 500, s.d. 18) in diameter and 145-155 μm (M = 150, s.d. 5) high, and about 5-7 cell filaments high. Conceptacle roofs formed by peripheral filaments; roof mound-like, peripheral part composed of filaments with cells 4-8 μm (M = 6, s.d. 2) long and 4-8 μm (M = 6, s.d. 2) in diameter; central part above chamber, about 30 μm thick, with pore canals 10-12 μm in diameter bordered by filaments 4-6 cells long.

Remarks: The occurrence of the monomerous coaxial thallus with cell fusions and the tetra/bisporangial multiporate conceptacles ascribes the specimens to the genus *Mesophyllum* (Woelkerling, 1988; Braga et al., 1993; Basso et al., 1998). In present-day *Mesophyllum* species, however, gametangial conceptacles are uniporate (Woelkerling, 1996). The occurrence of a coaxial core, considered thus far as diagnostic for *Mesophyllum*, has been recently discussed as far as its systematic value is concerned by Woelkerling & Harvey (1992, 1993) for Recent and by Basso et al. (1998) and by Braga & Aguirre (1998) for fossil material. The presence of a

coaxial core could not be used as the sole diagnostic character of *M.* while differences in spermatangial ontogeny and morphology did provide a basis for delimiting *Mesophyllum*, *Clathromorphum*, and *Synarthophyton* (Woelkerling & Harvey, 1992, 1993). This is confounded by the fact that populations of *M.* species often lack sexual characters (Keats & Chamberlain, 1994; Keats & Maneveldt, 1997). All present-day melobesioid species, however, which have a predominant coaxial core have been ascribed to *Mesophyllum*. The presence of a coaxial ventral core together with conspicuous cell fusions in fossil melobesioids are, in fact, the only readily preservable features available to separate *Mesophyllum* from other genera which share with it other vegetative characters such as monomerous construction and long subepithallial initials (Basso et al., 1998; Braga & Aguirre, 1998).

Mesophyllum sp. 1 is common in the foraminiferal-coralline algal, coralline algal, and grainstone facies. It is also present in the coralline algal-coral and coral facies. It only occurs as fragments of fruticose plants in which the conceptacles are very rare. Samples measured SLO94-043, SLO94-044, KO5, DU1.5.

Growth-form, thallus arrangement, and conceptacle characteristics of *M.* sp. 1 correspond to those described for *M.* sp. 1 from the Late Eocene of Lake Garda and Colli Berici (Bassi, 1995a, 1998). Bassi (1995a) compared *M.* sp. 1 from Colli Berici to *Lithophyllum simplex* Lemoine and *L. symetricum* Lemoine described and illustrated by Francavilla et al. (1970). These two species were determined by Francavilla et al. (1970) on the basis of thallus morphology and "hypothallial" cell size (p. 671 and p. 674). Francavilla et al. (1970) did not find conceptacle (see also the protologues in Lemoine, 1927, p. 548-549; Fig. 4).

Genus *Subterraniphyllum* Elliott, 1957

Type species: *Subterraniphyllum thomasii* Elliott, 1957

Taxonomic remarks: The genus was described by Elliott (1957) as a geniculate coralline alga. The taxonomic reassessment of this species and its circumscription based on the Elliott's type collection has been recently made (Bassi et al., 2000).

Subterraniphyllum thomasii Elliott, 1957

Pl. 5, fig. 7-8

v 1957 *Subterraniphyllum thomasi* Elliott 1957, p. 73-74, pl. 13, fig. 1-9.
1965 *Subterraniphyllum thomasi* Johnson, p. 812, pl. 100, fig. 6, 7.
1966 *Subterraniphyllum thomasi* Johnson, p. 277, pl. 6, fig. 1, 2.
1966 *Subterraniphyllum* (?) sp. indet. A - Beckmann & Beckmann, p. 30, pl. 8, fig. 112.
1968a *Subterraniphyllum thomasi* Mastrorilli, p. 388-390, pl. 41, fig. 1.
1968b *Subterraniphyllum thomasi* Mastrorilli, p. 1277-1280, pls. 101-103.
1977 *Subterraniphyllum thomasi* Lemoine, p. 34-36, pl. 3, fig. 10, 11.
2000 *Subterraniphyllum thomasii* Bassi et al., pls. 1-3.

Morphology: Plants with branching thalli ranging from 0.4 to 1.0 mm in diameter.

Vegetative anatomy: Pseudoparanchymatous, thalli with a monomerous cell arrangement. The core region consists of several filaments of cells (65-95 μm long and 45-65 μm in diameter) arranged more or less in tiers. Fusions between cells of adjacent filaments occur, but apparently in small numbers: in some fragments no cell fusions are observed. Cells resembling epithallial cells occur in 2-4 tiers (20-30 μm in diameter). Conceptacles are not present.

Remarks: This species has been recognized in the Oligocene of the Middle East (Persia and Oman; Elliott, 1957), Greece (Johnson, 1965), Borneo (Johnson, 1966), Cuba (Beckmann & Beckmann, 1966), Piedmont (Mastrorilli, 1968a, 1968b), Macedonia (Lemoine, 1977), and Colli Berici (Calcarenite di Castelgomberto, Veneto, northern Italy; Bassi et al., 2000). *S. thomasii* is present only in the sample SLO94-044 of the coralline algal-coral facies.

Geniculate corallines *sensu lato*
Pl. 5, fig. 4-6

Morphology: Plants arborescent branching, dichotomous thalli. Samples: KO2, KO5, KB2.1.

Remarks: Included are all geniculate fragments which, owing to the absence of the non-calcified genicula and conceptacles, remain unidentified. They are common in the grainstone facies and present in the coralline algal-coral facies.

Family S p o r o l i t h a c e a e Verheij, 1993
Subfamily S p o r o l i t h o i d e a e Setchell, 1943
Genus *Sporolithon* Heydrich, 1897

Type species: *Sporolithon ptychoides* Heydrich, 1897

Sporolithon sp. 1
Pl. 6, fig. 1-4

Morphology: Plants lumpy, warty, and more rarely encrusting, with typically swollen protuberances up to 3 mm long and 2 mm in diameter.

Vegetative anatomy: Monomerous non-coaxial thallus; core filaments about 100 μm thick, with cells 7-17 μm (M = 12, s.d. 5) long and 7-13 μm (M = 10, s.d. 3) in diameter; cell fusions abundant; peripheral filaments make up the thallus, cells square to elongate, 16-22 μm (M = 19, s.d. 3) long and 10-14 μm (M = 12, s.d. 2) in diameter; contiguous cells fused. No epithallial cells seen.

Uniporate sporangial compartments, 101-109 μm (M = 105, s.d. 4) high and 41-51 μm (M = 46, s.d. 5) in

diameter, with pore canal 8-13 μm (M = 11, s.d. 2) long, grouped in sori, consisting of about 26 sporangia, which raise about 12 cells above the thallus surface, and formed on a basal layer of elongated cells, 27-33 μm (M = 30, s.d. 3) long and 16-20 μm (M = 18, s.d. 2) in diameter. Old sori buried in the thallus. One to several calcified paraphyses, consisting of 5-7 elongate cells, 14-18 μm (M = 16, s.d. 2) long and 7-9 μm (M = 8, s.d. 1) in diameter, separate adjacent sporangial chambers.

Remarks: The species described here conforms to *Sporolithon* on the basis of non-coaxial core filaments, cell fusions, and sporangial compartments which may be solitary or aggregated into sori (Woelkerling, 1988, 1996; Braga et al., 1993; Keats & Chamberlain, 1993; Verheij, 1993; Townsend et al., 1995; Braga & Aguirre, 1998).

On the base of the characters used to identify the Recent species of *Sporolithon* (Verheij, 1992, 1993), some Palaeogene species from Veneto and Piedmont Basin ascribed to "*Archaeolithothamnium*" Rothpletz 1891 (Mastrorilli, 1958, 1968a, 1973) could be assigned to *Sporolithon aschersonii* (Schwager) Moussavian & Kuss (1990) (Bassi, 1995b, 1998). In the Poignant's (1985, p. 164) key for specific determinations of Cretaceous "*Archaeolithothamnium*", *Sporolithon aschersonii* (as '*Archaeolithothamnium aschersoni*') is characterized by a rare 'hypothallus', a 'threaded perithallus' with transversal partitions, and 'separated, non-merged sporangia'. These supposed key features are not however considered diagnostic in modern circumscription of both present-day and fossil *Sporolithon* species (see e.g. Verheij, 1993; Townsend et al., 1995; Braga & Aguirre, 1998). *S.* sp. 1 differs from *S.* cf. *aschersonii* described by Bassi (1998, p. 20, as '*S.* cf. *aschersoni*') in having higher tetra/bisporangial compartments (101-109 μm and 60-80 μm respectively) and more cells in the calcified paraphyses (5-7 and 4-5 respectively). This species is common in the coralline algal and coralline algal-coral facies and is present in the coral facies. Samples measured SLO94-043, SLO94-019, SLO94-21A, KO15, KB1.1, DU3.57.

Subclass **Florideophycidae** Schmitz in Engler, 1892
Order C r y p t o n e m i a l e s Schmitz in Engler, 1892
Family P e y s s o n n e l i a c e a e Denizot, 1968
Genus *Polystrata* Heydrich, 1905

Type species: *Polystrata dura* Heydrich, 1905

Polystrata alba (Pfender) Denizot, 1968
Pl. 6, fig. 5

1997 *Polystrata alba* (Pfender) - Bassi, p. 311-315, fig. 1-4 B.

Morphology: Very irregularly layered to foliose growth-forms with numerous superimposed encrusting layers that can develop into small ellipsoidal. The narrow cavities between each layer can be filled with micrite.

Vegetative anatomy: Epigenous plants made up of thin flattened or curved branches (lamellate *sensu* Woelkerling et al., 1993, p. 280) forming variously shaped thalli lacking protuberances. The thallus is pseudoparenchymatous, composed of filaments and organised in a bilateral-radial manner. In longitudinal section, each thallus (400-500 μm thick) consists of a single eccentric row (closer to the ventral part of the crustose thallus) of primigenous filaments composed of tall cells, 46-54 μm (M = 50; s.d. 4) long and 27-33 μm (M = 30, s.d. 3) in diameter, joined by primary pit-connections. Postigenous filaments arise plumosely from the outer surface of the cells of primigenous filaments both upward and downward; columnar cells 38-42 μm (M = 40, s.d. 2) long and 8-12 μm (M = 10, s.d. 2) in diameter; successive cells are joined by primary pit-connections. The surface of each thallus is characterised by epithallial cells that are smaller than those below. Longitudinal sections show the bilateral-radial organisation of the thallus. Transverse sections show the contiguous primigenous and postigenous filaments. No conceptacles found.

Remarks: The vegetative anatomy of this peyssonneliacean species has important analogies with those of the non-geniculate corallines. All the descriptions of this species in the literature are based on the traditional terminology used for the coralline red algae (i.e. hypothallium and perithallium), which tends to obscure the fundamentally filamentous nature of the thallus. For this reason, Bassi (1997) described its vegetative anatomy using the terminology adopted for the present-day non-geniculate corallines by Woelkerling & Irvine (1988). The fossil record of *P. alba* extends from the Early Cretaceous (Urgonian facies in Pfender, 1936; Massieux & Denizot, 1964) to the Oligocene (Mastrorilli, 1968a; Bassi, 1997). *P. alba* facies (*Pseudolithothamnium album* or *Ethelia alba* facies *Auctorum*) have been also described from the Late Cretaceous of Istria, Croatia (Drobne et

al., 1988, 1989), from the Palaeocene of Dalmatia, Croatia (Šikic & Šikic, 1978) and Trieste area (SB4; Brazzati et al., 1996), from the Early Eocene of southern Slovenia (Jurkovsek et al., 1996), from the Early-Middle Eocene of Krappfeld (Austria; Rasser, 1994), and from the Late Palaeocene of the Apennines (Praturlon, 1966; Pignatti, 1994).

This species is not common, but present in the coralline algal, coralline algal - coral and coral facies. Samples measured: KO15, SLO94-015, DU1.4, DU3.3.

Division **Chlorophyta** Papenfuss, 1946

Class C h l o r o p h y c e a e Kützing, 1843

Family H a l i m e d a c e a e Link, 1832

Genus *Halimeda* Lamouroux, 1812

Halimeda sp. 1
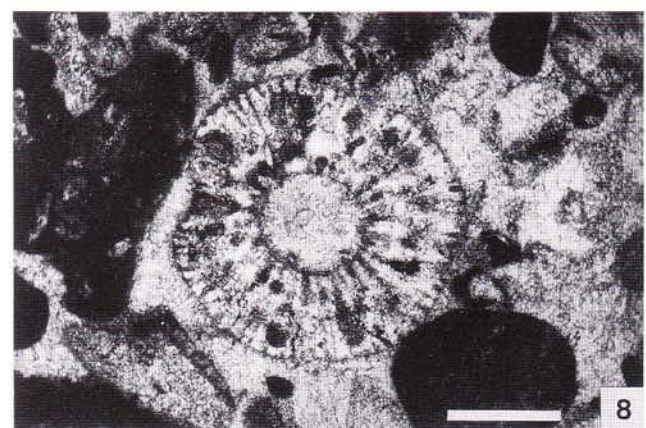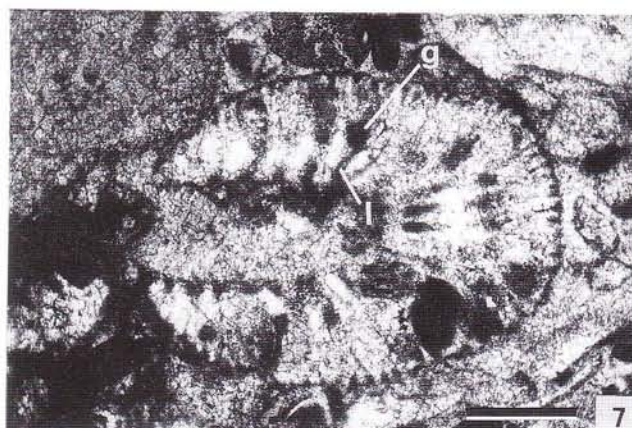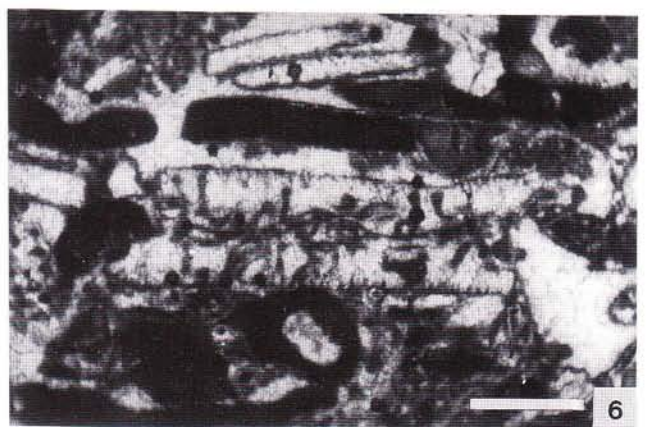
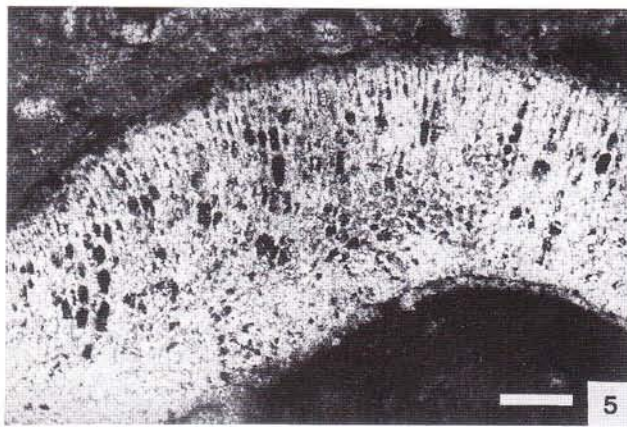Pl. 6, fig. 6

Morphology: Fragments of flattened segments.

Vegetative anatomy: Thallus consists of medullary interwoven tubes, about 30 μm in diameter, arranged subparallel to the main axis of the thallus. They branch about two times before reaching the thallus surface where the cortical terminations are represented by pores about 20 μm in diameter.

Remarks: According to Bassoulet et al. (1983), the genus is represented by twelve fossil species and has a stratigraphic range extending from the Cretaceous to the Recent (e.g. Johnson, 1961; Beckmann & Beckman, 1966; Bassoullet et al., 1983; Flügel, 1988; Mu, 1991). Upper Palaeogene *Halimeda* species have been described from the Middle-Late Eocene of China (*H. lingulata*, in Bassoullet et al., 1983) and from the Oligocene of Cuba (*H.* species in open nomenclature; Beckmann & Beckman, 1966). No species so far described in the Oligocene deposits of the Mediterranean area shows characters comparable to *H.* sp. 1.

This species is only present in the grainstone facies; sample: KO6.

PLATE 6

Fig. 1   - *Sporolithon* sp. 1, thallus protuberance showing transversal (t) and longitudinal (l) sections of sporangial sori, DU13; scale bar = 500 μm.

Fig. 2   - *Sporolithon* sp. 1, longitudinal section through a sporangial sorus showing the basal layer of elongated cells (arrow), DU1.22; scale bar = 200 μm.

Fig. 3   - *Sporolithon* sp. 1, 5 to 7 celled paraphyses (arrow) and elongated cells (ec) above the basal layer (bl, smallest arrow), SLO94-019; scale bar = 100 μm.

Fig. 4   - *Sporolithon* sp. 1, non-coaxial core region (c) and peripheral region with sporangia, SLO94-019; scale bar = 100 μm.

Fig. 5   - *Polystrata alba* (Pfender) Denizot, longitudinal section of a thin crust showing the postigenous cell filaments, SLO94-015 scale bar = 100 μm.

Fig. 6   - *Halimeda* sp. 1, oblique longitudinal section, KO6; scale bar = 400 μm.

Fig. 7   - *Cymopolia* sp. 1, oblique section showing gametophores (g) terminal in position on primary laterals (l) and along their axis, DU3.91; scale bar = 400 μm.

Fig. 8   - *Cymopolia* sp. 1, transversal section, DU3.91; scale bar = 400 μm.
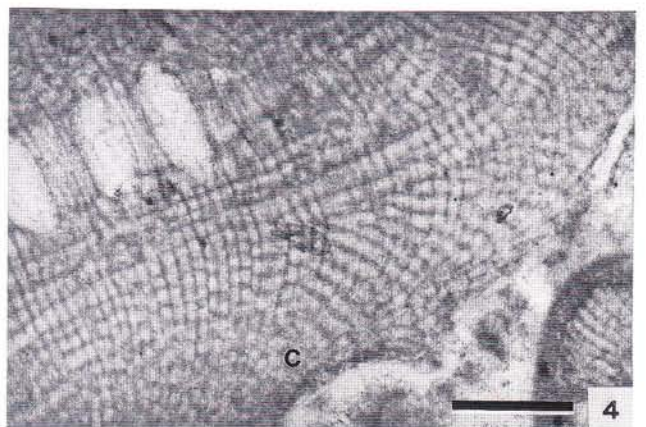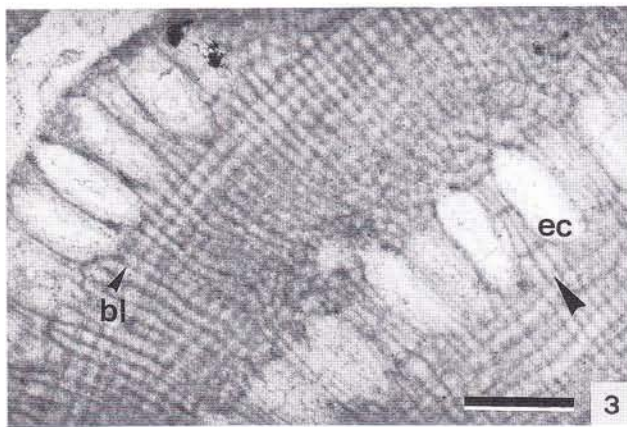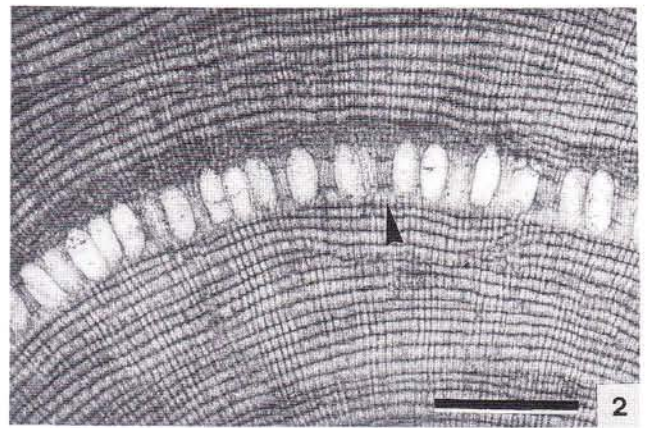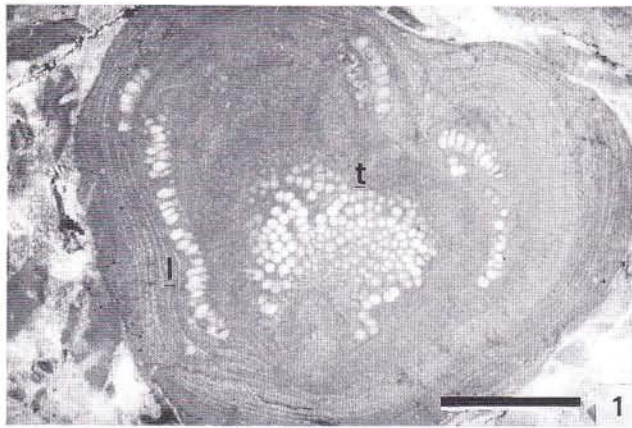
Order D a s y c l a d a l e s Pascher, 1931

Family D a s y c l a d a c e a e (Kützing 1843)

emend. Berger & Kaever, 1992

Tribe Dasycladeae Pia, 1920

Genus *Cymopolia* Lamouroux, 1816

Cymopolia sp. 1

Pl. 6, fig. 7-8

Morphology: Plant with a central stem, laterals and gametophores.

Vegetative anatomy: Primary laterals of central whorls of one article composed of a moderately long peduncle followed by a swollen portion, phloiophorous, about 1/3 of the whole lateral length. Primary laterals of apical and basal whorls more slender and long. Reproductive organs made by ovoid gametophores terminal on primary laterals. Secondary laterals longer than primary ones. Only three transversal and oblique sections were found.

Remarks: A few dasycladalean genera which appeared during the Mesozoic have Cenozoic representatives. Two of them, *Cymopolia* Lamouroux and *Neomeris* Lamouroux, are still extant. The stratigraphical range of *Cymopolia* spans from the uppermost Early Cretaceous to the Recent (Barattolo, 1991); the maximum peak diversity of the genus occurred during the Middle Eocene (Lutetian; Deloffre & Granier, 1992). Three species have been described so far of possible Oligocene age [*C. elongata* (Defrance in Bronn, 1825) Munier-Chalmas 1877, *C. pacifica* Johnson 1957, and *C. zitteli* Munier-Chalmas ex Morellet & Morellet 1913], although Deloffre & Granier (1992) questioned the exact stratigraphy of these findings. Only three calcareous skeletons of *C.* sp. 1 were found in random thin sections in the grainstone microfacies. Neither a detailed reconstruction of the skeleton nor a biometrical analysis were possible considering the rare random sections of the thallus. This species is only present in the grainstone facies; sample: DU3.91.

Concluding remarks.

(1) The excellent preservation of a number of vegetative and reproductive features of the fossil coralline red algae from the Early Oligocene of northern Slovenia allowed the application of the systematics of Recent representatives at the genus level. Seven Corallinaceae red algal genera (*Lithoporella, Neogoniolithon, Spongites, Lithothamnion, Mesophyllum, Sporolithon, Subterraniphyllum*) have been recognized. A peyssonneliacean (*Polystrata alba*) and two green algae (the dasycladacean *Cymopolia* sp. 1 and the halimedacean *Halimeda* sp. 1) are also present.

(2) The coralline red algal species are named following an open nomenclature because of the lack of revisions of the type collections of fossil material. A reliable re-identification of the coralline species based solely on published descriptions is not possible. Rigorous revisions of original collections are needed to precisely describe fossil coralline algal taxa in terms of modern phycological taxonomic concepts (neontological approach). In the absence either of comparative studies of nomenclatural types and of relevant information on critical characters, only very limited comparisons are possible, and in most cases no definitive taxonomic conclusions can be reached.

(3) There is a considerable variation in growth-forms at both genus and species level. This corresponds to similar findings for Recent coralline algae and demonstrates the inconsistency in using growth-forms as diagnostic characters for specimens identification.

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