Fossil coralline algae from the Paleocene Montorfano Member type-section (Tabiago Formation, northern Italy)

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ABSTRACT

Seven species of fossil Corallinales (Rhodophyta) from the Montorfano Member type-section (Tabiago Formation, Late Paleocene, northern Italy) are circumscribed and discussed using some of the diagnostic criteria applied for present-day corallines. Favourable circumstances, among which principally the partial preservation of epithallial cells (usually destroyed by abrasion or bioerosion), enabled us to describe two species referring to the genus *Phymatolithon*; besides these, one species of *Lithothamnion*, two of *Mesophyllum* and two of *Sporolithon* have been separated. Within the considered re-sediments, the Corallinales usually occur as broken-off thalli; nevertheless, two crustose species (*Mesophyllum* sp.1 and *Sporolithon* sp.1), have been recognized as important builders of re-deposited spheroidal rhodoliths. Furthermore, the present paper highlights that, if a well-preserved fossil material is available, some conclusive features used in the neontological taxonomy, among which the relative length of the subephitallial initials and, less frequently, the shape of the overlying epithallial cells, can be recognized with confidence even using an optical microscope instead of requiring SEM observations.

RIASSUNTO

Sette specie di alghe Corallinales fossili (Rhodophyta) provenienti dalla sezione-tipo del Membro di Montorfano (Formazione di Tabiago, Paleocene, Comasco) vengono delimitate ed esaminate applicando alcuni criteri diagnostici della moderna sistematica relativa alle forme viventi. Circostanze favorevoli, tra cui principalmente la conservazione delle fragili cellule epitalliche, generalmente distrutte dall'abrasione o dalla bioerosione, hanno consentito di caratterizzare due specie appartenenti al genere *Phymatolithon*; oltre ad esse vengono anche descritte una specie di *Lithothamnion*, due specie di *Mesophyllum* e due di *Sporolithon*. All'interno dei sedimenti considerati, le Corallinales si rinvengono generalmente come frammenti di talli, tuttavia due specie (*Mesophyllum* sp.1 e *Sporolithon* sp.1), intervengono in modo importante nella costruzione di rodoliti sferoidali a morfologia laminare.

Infine, viene sottolineato che, qualora sia disponibile un materiale fossile ben conservato, l'uso del microscopio ottico risulta sufficiente a descrivere alcuni caratteri considerati decisivi dalla moderna tassonomia delle forme viventi, tra cui soprattutto la lunghezza relativa delle cellule subepitalliche e più raramente la forma delle sovrastanti cellule epitalliche, senza che ciò richieda necessariamente l'applicazione delle tecniche SEM.

1. Introduction

The present contribution explores the possibility to apply neontological criteria to a nongeniculate coralline red algae assemblage from the Paleocene Montorfano Member of the Tabiago Formation (Como, northern Italy) (Fig. 1).

A general revision of the coralline red algae taxonomy is in progress as a consequence of new diagnostic criteria recently proposed. This involves also the paleontological classification, traditionally separate from the neontological one (Wray 1977, Poignant 1984), since recent studies have demonstrated the fossilisation potential of some diagnostic features used as taxonomic criteria in present-day corallines (e.g. Bosence 1991, Braga et al. 1993, Rasser & Piller 1999). At generic level, these features are especially related to the cell connections between contiguous filaments (i.e. interfilamental cell fusions or secondary pits), to the shape of the epithallial cells and to the relative length of the subepithallial initials (i.e. meristematic cells whose continued division increases the thallus surface). For a long time, the epithallial cells in particular have commonly been regarded by paleoalgologists as not mineralized and therefore unpreservable. In reality, they conserve their lateral walls but are not firmly calcified at their uppermost surface (Cabioch & Giraud 1986) and, as a consequence, their shape usually does not appear definable with confidence (Basso 1995). At any rate, the epithallus protects the underlying subepithallial initials and makes them recognizable. In the studied material, the preservation of the above-mentioned characters allowed to circumscribe fossil genera using, together with some traditional features, also most concepts applied to present-day corallines. Further criteria in agreement with Rasser & Piller (1999) have been used to separate species within each genus; these criteria are discussed in the systematic descriptions.

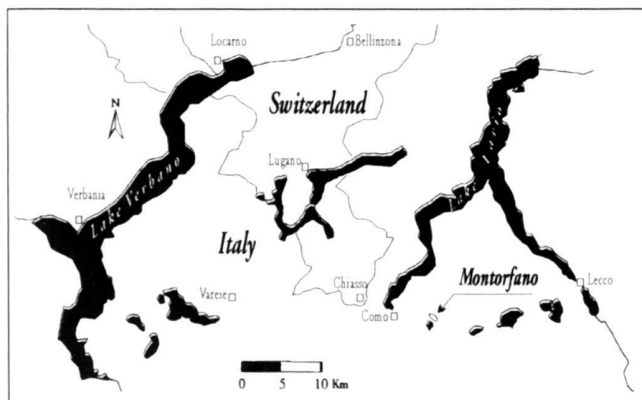GeoLogica, CH - 6673 Maggia, Switzerland. E-mail: rudolf.stockar@span.ch.

Fig. 1. Location of the Montorfano Member type-section.

2. Geological background

Between Como and Bergamo, along the southern border of the Alps, some Lower Tertiary outcrops are spread. They consist of a variety of sediments which have been separated on lithologic and faunistic grounds by Kleboth (1982) and, keeping them together, by the same author defined as Tabiago Formation. This formation reaches a thickness of over 100 m and includes hemipelagic sediments with interbedded thin carbonate turbidites. In its upper part, the Tabiago Fm. comprises ruditic to arenitic calcareous re-sediments which may locally dominate. This is the case, as an example, of the Monte Giglio section, whose algal assemblage has been described by Beckmann et al. (1982), and particularly of the Montorfano section, with which several authors dealt in the past (Buxtorf & Reichel 1936; Lanterno 1958; Hottinger 1960; Bichsel 1977; Kleboth 1982 among others). In the Montorfano section the hemipelagic marls are virtually absent and, for this peculiarity, Kleboth (1982) defined this sequence as a separate member within the Tabiago Fm.. The type-section of the Montorfano Member reaches a total thickness of about 120 m and makes up entirely an isolated hill rising out of the Quaternary plain deposits five kilometres south-east of Como (Fig. 1–2). It consists of proximal and channelized carbonate re-sediments, predominantly including calcarenites and calcirudites crowded with shallow-water biota, among which calcareous red algae are very frequent. Taking into account the presence, among the displaced microfossils, of larger foraminifera such as *Glomalveolina primaeva* Reichel (reported in Hottinger 1960) and *Nummulites* cf. *deserti* De la Harpe (at the top of the section, recorded in Bichsel 1977), a Late Paleocene age (likely span-
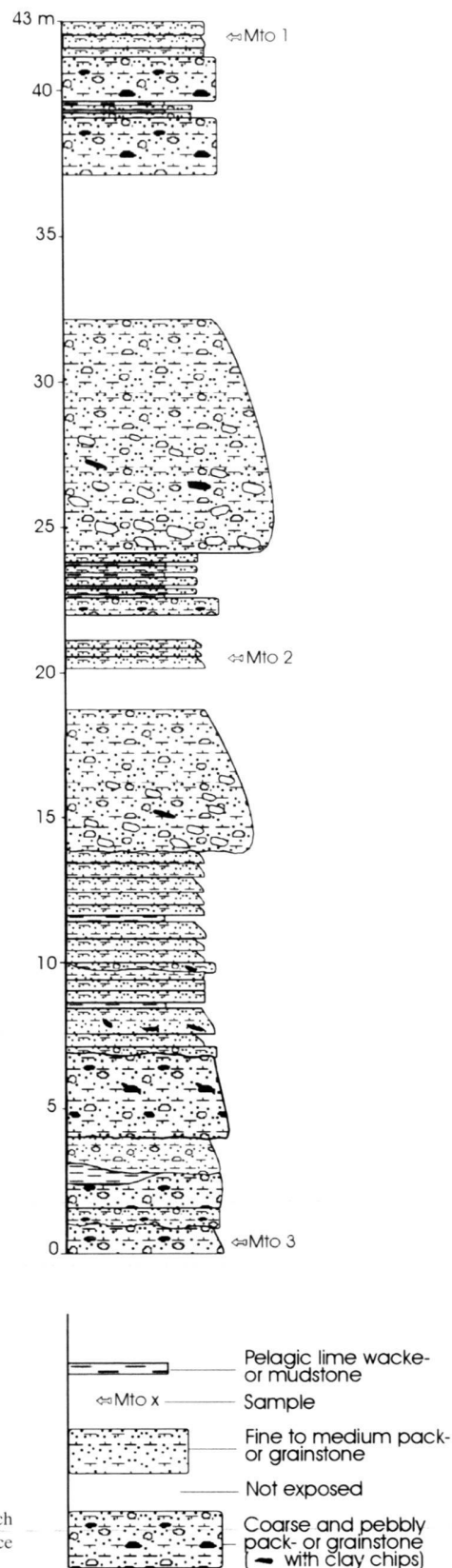
Fig. 2. Stratigraphic section through the quarry close to the village of Montorfano, from which the samples described in the present paper come (after Kleboth 1982, redrawn). This sequence corresponds to the uppermost part of the whole Montorfano Member type-section.
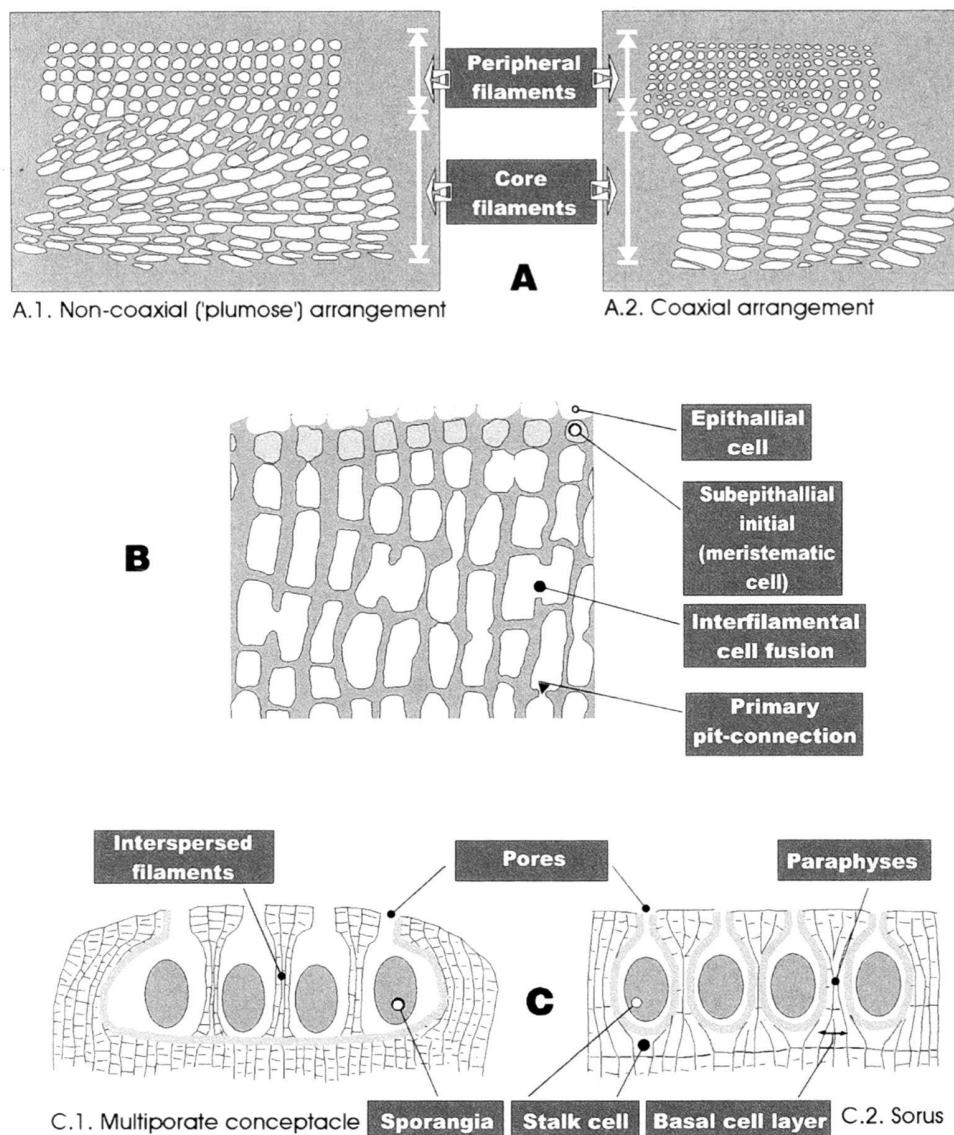
A.1. Non-coaxial ('plumose') arrangement   A.2. Coaxial arrangement

C.1. Multiporate conceptacle   Sporangia   Stalk cell   Basal cell layer   C.2. Sorus

Fig. 3. Main taxonomic features of coralline algae reported in the present paper.
(A) Inner cell arrangements in monomerous thalli.
(B) Detail of the uppermost portion of peripheral filaments.
(C) Asexual reproductive organs.

ning from SBZ 3 to SBZ 5 sensu Serra-Kiel et al. 1998) may be postulated for these allochtonous biota. The scanty in situ microfaunas, including planktic foraminifera determined by Kleboth (1982), are of virtually the same age as the over-mentioned displaced shallow-water forms.

3. Material and methods

All the specimens described in this paper come from the channelized deposits cropping out at the abandoned quarry close to the village of Montorfano, on the southern side of the hill. This quarry is one of the three outcrops through which the type-section was originally drawn and offers an unweathered sequence of the youngest part of the Montorfano Member (Fig. 2). Samples were taken, respectively at the bottom, middle and top of the section. The first sample (Mto3, bottom of the section) comes from pebbly biocalcarenitic bodies in which re-deposited rhodoliths are seldom scattered. These red algal nodules show a spheroidal geometry (diameter never exceeding 8 cm) and a laminar growth morphology (Bosence 1983) (Pl. 1, Fig. 1) starting from a bioclastic nucleus, commonly represented by a coral fragment; in some cases, nuclei are dissolved and the voids are filled with sediment. In the rhodoliths, nongeniculate crustose coralline algae occur together with peyssonneliacean algae and acervulinid foraminifera; in addition, segments of geniculate coralline and fragments of green algae are scattered inside the sediment-filled voids. The algal content of the second (Mto2, middle of the section) as well as of the third sample (Mto1, top of the section), both coming from grainstone beds, is very abundant but consisting only of

Lithothamnion sp.		Range	M	SD	V	CI
Ventral core	L	12-22	16.7	3.1	0.19	15.5-17.9
	D	6-11	8.4	1.1	0.13	8.0-8.8
Peripheral region	L	8-14	10.6	2.0	0.19	9.9-11.3
	D	7-9	7.9	0.5	0.06	7.7-8.1
Conceptacles	H	100-130	122	11.0	0.09	118-126
	D	200-320	261	44.1	0.17	244-277
Roof thickness		32-56	37.7	9.5	0.25	34.2-41.2

Phymatolithon sp.1		Range	M	SD	V	CI
Ventral core	L	12-20	16	3.4	0.21	14.7-17.3
	D	8-10	9	1.0	0.11	8.6-9.4
Peripheral region	L	9-16	13.6	1.8	0.13	12.9-14.3
	D	8-12	10.0	1.8	0.18	9.3-10.7
Conceptacles	H	64-102	99	6.9	0.07	96-101
	D	136-360	271	82.6	0.30	240-302
Roof thickness n=4		28-29	28.5	0.6	0.02	28.3-28.7

Phymatolithon sp.2		Range	M	SD	V	CI
Ventral core	L	10-16	13.3	2.6	0.20	12.3-14.3
	D	10-13	11.5	1.5	0.13	10.9-12.1
Peripheral region	L	10-14	12.3	1.4	0.11	11.8-12.8
	D	8-12	9.2	1.5	0.16	8.6-9.8
Conceptacles	H	64-72	67.7	4.1	0.06	66-69
	D	224-272	248	24.4	0.10	239-257
Roof thickness		Measurements not available				

Mesophyllum sp.1		Range	M	SD	V	CI
Ventral core	L	12-24	18.1	3.1	0.17	16.9-19.3
	D	7-9	7.9	0.6	0.08	7.7-8.1
Peripheral region	L	7-10	9.0	1.1	0.12	8.6-9.4
	D	6-8	7.4	0.9	0.12	7.1-7.7
Conceptacles	H	130-160	146	7.3	0.05	143-148
	D	320-500	414	45.7	0.11	397-431
Roof thickness		32-52	41.3	7.4	0.18	38.5-44.1

Mesophyllum sp.2		Range	M	SD	V	CI
Ventral core	L	12-22	17.7	3.6	0.20	16.4-19.0
	D	9-12	10.8	1.1	0.10	10.4-11.2
Peripheral region of protuberances ('cortex')	L	8-14	9.8	1.6	0.16	9.2-10.4
	D	8-9	8.5	0.5	0.06	8.3-8.7
Peripheral region of crusts and central core of protuberances ('medulla')	L	15-24	19.9	3.2	0.16	18.7-21.1
	D	9-11	10.5	0.6	0.06	10.3-10.7
	l	8-14	10.2	1.8	0.18	9.5-10.0
	d	8-10	9.0	1.0	0.11	8.6-9.4
Conceptacles	H	110-140	134	12.2	0.09	129-139
	D	230-340	278	54.9	0.20	258-299
Roof thickness n=8		20-22	20.9	1.0	0.05	20.5-21.3

Sporolithon sp.1		Range	M	SD	V	CI
Ventral core	L	12-24	18.3	4.5	0.25	16.6-20.0
	D	8-10	8.9	1.0	0.11	8.5-9.3
Peripheral region	L	8-12	9.2	1.5	0.16	8.6-9.8
	D	8-10	9.4	0.6	0.06	9.2-9.6
Sporangia	H	64-80	74.0	6.5	0.09	72-76
	D	32-38	35.3	2.5	0.07	34-36

Sporolithon sp.2		Range	M	SD	V	CI
Ventral core		Measurements not available				
Peripheral region	L	12-18	15.3	2.5	0.16	14.4-16.2
	D	8-10	8.6	0.8	0.09	8.3-8.9
Sporangia	H	64-80	73.6	4.4	0.06	72-75
	D	32-34	33.0	1.0	0.03	33

L: Length (cells)
D: Diameter (cells and reproductive organs)
H: Height (reproductive organs)
M: Mean
SD: Standard Deviation
V: Variability
CI: 95 % Confidence Interval

With regard to *Mesophyllum* sp.2, the sizes of the largest (L,D) and of the smallest (l,d) cells, in peripheral region of crusts and in the central core of protuberances, are given separately.

For each feature 30 measurements (n) have been performed, unless otherwise stated.

All measurements are given in micrometers (μm).

fragments. Besides the nongeniculate coralline algae, the fossil content includes geniculate coralline, peyssonneliacean and solenoporacean algae, green algae, bryozoans, echinoid plates and spines, small benthic foraminifera (miliolids and rotaliids).

In the present work, fossil algae have been studied in thin section using a petrographic optical microscope. Although no SEM observations were carried out, it was nevertheless possible to apply modern taxonomic criteria; this was made easier by the good state of preservation of fossil material, in which the delicate epithallus could have been sometimes protected from erosion by the overgrowth of later algal crusts. Whereas it was rather difficult to perform thorough observations concerning the shape of the epithallial cells, the occurrence of cell fusions and the pattern of the subepithallial cell elongation readily appeared clear enough to allow generic assignments. For all the cells making up the pseudoparenchyma (i.e. the aggregation of branching filaments which constitutes the thallus), L denotes the distance between two primary pit-connections (length of the cells) and D means the distance between the median lines of lateral walls (diameter of the cells). As far as the reproductive organs are concerned, D and H denote respectively the internal maximum diameter and maximum height of the chambers; only asexual organs have been observed. For each feature thirty measurements have been performed; where only fewer measurements were possible, the number of observations (n) has been reported. Afterwards, the arithmetical mean (M), the standard deviation (SD), the variability (V) and the 95 percent confidence interval (CI, derived from the Student function), have been calculated. All biometrical measurements and statistical data are listed in Table 1.

The generic and supra-generic classification scheme, thallus nomenclature, diagnostic features and growth form definitions follow Woelkerling (1988), Braga et al. (1993), Woelkerling et al. (1993) and Rasser & Piller (1999). The main taxonomic features described in the studied material are briefly summarized in Fig. 3. It is worth mentioning that the majority of the known fossil coralline species have been established a long time ago by focusing on criteria different from those considered relevant in modern taxonomy. A revision of the types of fossil corallines on the basis of present-day taxonomic concepts began only in the last decade (e.g. Moussavian & Kuss 1990; Aguirre & Braga 1998; Basso et al. 1998) and is still in progress. Without a re-description of the original collections, most names of fossil taxa are still lacking in precise meaning and, until their revision upon modern criteria has been undertaken, the use of them should be made with great circumspection or simply avoided. This appears to be confirmed by the first results of the re-documentation works, which on the one hand led to changes of generic and family assignment for some fossil coralline species and, on the other hand, highlighted the uncertain nature of some other algal taxa in consequence of the lack of sufficiently conclusive diagnostic characters (e.g. Aguirre & Braga 1998). For these reasons, in the present paper an open nomenclature has been preferred instead of choosing specific names from those reported in the abundant literature which is often too old and, as a consequence, not always conclusive enough within the framework of the modern taxonomic concepts. However, as far as the described species are concerned, some analogies with species established in traditional literature have tentatively been drawn; a particular comparison has been made with respect to the algal assemblage from the Paleocene Monte Giglio section (Beckmann et al. 1982), since it represents the best-known carbonate sequence belonging to the Tabiago Formation.

Thin sections containing described and figured specimens will be deposited at the Natural History Museum, Lugano, Switzerland. Their labels (e.g. Mto1A) mean as follows: Mto = Montorfano quarry, number = sample (see Fig. 2), letter = thin section.

4. Systematic descriptions

Division Rhodophyta Wettstein 1901
Class Rhodophyceae Rabenhorst 1863
Order Corallinales Silva & Johansen 1986
Family Corallinaceae Lamouroux 1812
Subfamily Melobesioideae Bizzozero 1885

Genus *Lithothamnion* Heydrich 1897
Lectotype species: *L. muelleri* Lenormand ex Rosanoff 1866

Diagnostic features preservable in fossil material

Thallus nongeniculate, internal construction monomerous, core filaments non-coaxial, cells of adjacent filaments joined by fusions, secondary pit connections (i.e. between adjacent filaments) absent, epithallial cells flattened (frequently appearing flared), meristems with cells as long as or longer than their immediate inward derivatives, multiporate asexual conceptacles.

Remarks

Within the monomerous-type melobesioids, flared epithallial cells are regarded as peculiar to *Lithothamnion* Heydrich (nom. cons. in substitution of *Lithothamnium* Philippi). According to Rasser & Piller (1999), the circumscription of fossil species mainly focuses on such features as thickness and cell size of both core and peripheral portions, occurrence and thickness of growth rhythms, conceptacle size, size of the cells in the conceptacle roof and its thickness, pore size, occurrence of a rimmed conceptacle roof, amount to which conceptacle protrude above the original thallus surface. Growth form differences, though widely used in the past, are presently regarded as a poor diagnostic feature in delimiting species, since they are strongly influenced by various environmental gradients (e.g. Woelkerling et al. 1993, Bassi & Nebelsick 2000). However, within a given assemblage related to a particular environment, also morphological variations may be helpful in specimen identification.

Lithothamnion sp.
(Tab. 1; Pl. 1, Fig. 2–5).

Description

Growth form encrusting to warty with up to 2.5 mm long and up to 2.1 mm wide protuberances (Pl. 1, Fig. 2). The thallus is pseudoparenchymatous with dorsiventral organisation (i.e. arrangement in which a distinct upper and lower surface can be distinguished) of monomerous type (i.e. in which a single system of cell filaments contribute both to a core and to a peripheral region). Thin, non-coaxial ventral core up to 70 µm thick (Pl. 1, Fig. 3). Some derivatives of the core filaments roughly curve outwards forming the peripheral region, while other derivatives only very faintly curve towards the substrate. The longest cells occur in the basal part of the core. Peripheral region with distinct lenticular growth zones 60–120 µm thick, mostly consisting of 6–8 cell layers; these are longer in the fertile portions of the thallus than in the sterile ones. Cell fusions are evident in the peripheral region, especially in fertile portions, and also occur in the ventral core region. The epithallus is one cell-layer thick and is rarely preserved (Pl. 1, Fig. 4). Its cells are flattened with flared distal walls, 7–8 µm in diameter and 4–5 µm long. Subepithallial initials are as long as or slightly longer than the cells immediately subtending them. Sporangia conceptacles multiporate, rectangular to elliptical in longitudinal section (Pl. 1, Fig. 5), with rounded lateral walls and flat to weakly convex roof, commonly composed of 4–5 cell layers. Roof thickness 32–56 µm, pore diameter 14–24 µm. The conceptacle floor is usually 2–3 cell layers below the original thallus surface and, consequently, these reproductive organs appeared, at the time of their formation, in all likelihood only just slightly sunken. Owing to the presence of these conceptacles virtually protruding above the surrounding surface, the subsequent overgrowth of peripheral cell filaments had to overlie them lending a wavy appearance to the peripheral region (Pl. 1, Fig. 2). Many buried conceptacles (Pl. 1, Fig. 5) are partially filled with large cells of elongate to irregular shape, which may be interpreted as re-crystallized remains of interspersed filaments. Some formations hanging from the roof of empty conceptacles are probably due to the growth of bundles of calcite crystals after the spore release. Furthermore, two ovoid structures occurring inside one conceptacle might represent remains of sporangia.

Remarks

The presence of highly diagnostic features, such as flat and flared epithallial cells and subepithallial initials as long as or longer than their immediate inward derivatives, leaves no doubt as to the belonging of this melobesioid alga to the genus _Lithothamnion_ Heydrich. Habit, structure and cell biometry show many affinities with _Lithothamnion roveretoi_ Airoldi 1932 but the original material of Airoldi exhibits a generally larger conceptacle size; at any rate, a certain assignment to this species is not possible without a re-description of its type ma-

terial focused on modern taxonomic concepts. Moreover, this form might correspond to the species reported from the Monte Giglio section (Beckmann et al. 1982) as '_Lithothamnium_ cf. _wallisium_ Johnson & Stewart' which, however, may exhibit more varying conceptacle size. Among the fossil species described recently on the basis of neontological criteria (Bassi 1998, Bassi e Nebelsick 2000) many vegetative analogies can be drawn between the specimens described here and _Lithothamnion_ sp.2 from the Lower Oligocene of Slovenia (Bassi e Nebelsick 2000). This latter, however, persistently exhibits larger (D 337–347 µm versus 200–320 µm) and higher (130–140 µm versus 100–130 µm) conceptacle chambers and, consequently, cannot be regarded as co-specific to _Lithothamnion_ sp.

Lithothamnion sp. is abundant in the studied material; it occasionally forms rhodoliths in association with _Mesophyllum_ sp.1 and _Sporolithon_ sp.1 but more frequently occurs only as small fragments. Occurrence: thin sections Mto1A, Mto1B, Mto2, Mto3A, Mto3B.

Genus _Phymatolithon_ Foslie 1898
Type species _P. calcareum_ (Pallas) Adey & McKibbin 1970

Diagnostic features preservable in fossil material

Thallus nongeniculate, internal construction monomerous, core filaments non-coaxial, interfilamental cell fusions present, secondary pits absent, epithallial cells rounded or flattened but not flared, meristems with cells as short as or shorter than their immediate inward derivatives, multiporate asexual conceptacles.

Remarks

Prior to the 1990's, in agreement with the traditional criteria for fossil coralline algae, the specimens here assigned to the genus _Phymatolithon_ would have been ascribed to the genus _Lithothamnion_ (Wray 1977). In accordance with the modern generic concepts, the occurrence of flattened to rounded in shape but never flared epithallial cells and the presence of subepithallial initials shorter than cells immediately underneath allow a sharp separation from other melobesioids (including _Lithothamnion_) and impose the assignment to _Phymatholiton_. Only _Leptophytum_ Adey has similar characters as _Phymatoliton_ but there is presently some controversy as to whether it is a genus distinct from _Phymatoliton_. At any rate, since _Leptophytum_ and _Phymatoliton_ share all diagnostic features with fossilisation potential, in fossil material they would be indistinguishable from each other (Braga et al. 1993). Recently, Rasser & Piller (1999) described an Eocene _Phymatholithon_ species which, however, shows analogies with neither of the species reported here. The identification of fossil species within the genus _Phymatholithon_ has been carried out taking into account the same specific characters as those already described with respect to _Lithothamnion_.
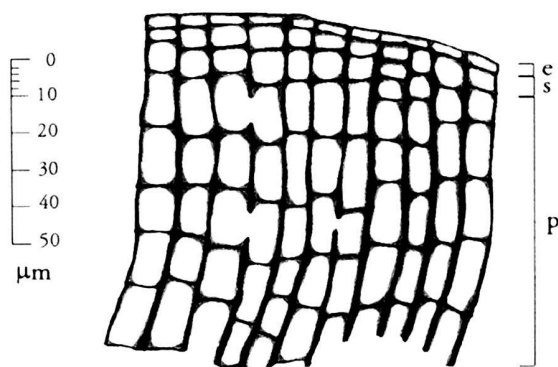
Fig. 4. *Phymatolithon* sp.1. Section of thallus showing epithallial cells (e) and subepithallial initials (s); these latter are as short as or shorter than the cells subtending them (p). Thin section Mto1A (same specimen as Plate 1. Fig. 7).

Phymatolithon sp. 1
(Tab.1; Fig. 4; Pl.1, Fig. 6–7)

Description

Only warty fragments occur, with up to 1.7 mm long and up to 1.1 mm wide protuberances. The thallus is pseudoparenchymatous with dorsiventral organisation of monomerous type. Ventral core with non-coaxial organization. Only poorly preserved core filaments, overgrowing damaged portions inside the peripheral region, are measurable. Core filaments roughly curve outwards forming the peripheral region, while they never curve downwards. The longest cells occur in the basal part of the core. Peripheral region with well-developed irregular growth zones, each consisting of four to seven layers of rectangular thick-walled cells (Pl. 1, Fig. 6); cell fusions are evident. The epithallus consists of one layer of very flattened to slightly rounded, horizontally elongated cells, 8–12 μm in diameter and 3–5 μm long. Dividing vegetative initials are as short as or shorter than cells immediately subtending them (Fig. 4; Pl. 1, Fig. 7). Sporangia conceptacles multiporate; in longitudinal section their outline appears approximately rectangular with rounded corners. The roof is commonly flat, thin and consists of 3 layers of unusually short cells (length 9 μm). Roof thickness 26–28 μm, pores not clearly visible. Conceptacle were completely raised above the thallus surface at the stage they were formed and, consequently, after their burial by later plant growth, growth rhythms became more irregular and lenticular. Conceptacles are partially filled with large cells of elongate to irregular shape which might represent poorly preserved remains of interspersed filaments.

Remarks

This species is rare and occurs only as small fragments. From the Monte Giglio assemblage only specimens described as 'Lithothamnium cf. *camarasae* Pfender' and 'Lithothamnium

sp. indet. A' (Beckmann et al. 1982) roughly exhibit similar growth form and zonation but differ from *Phymatholithon* sp.1 in biometrical data. Occurrence: thin sections Mto1A, Mto1B.

Phymatolithon sp. 2
(Tab. 1; Pl. 2, Fig. 1–2)

Description

Fragments with warty growth form consisting of stumpy protuberances up to 1.7 mm long and up to 1.8 mm wide. The thallus is pseudoparenchymatous with dorsiventral organisation of monomerous type. Filaments of the basal ventral core non-coaxially arranged but poorly preserved. Measurements refer to core filaments overgrowing damaged portions inside the protuberances. Core filaments bend outwards forming the peripheral region, while they never curve towards the substrate. The longest cells occur in the basal part of the core. Peripheral region zoned (Pl. 2, Fig. 1), each growth zone consisting of 5–9 layers of cells often laterally joined by fusions. The zonation is due to a gradual decrease in cell size from the bottom to the top of each zone; the longest cells of younger growth zones appear abruptly superimposed on the smallest cells of the previous zones. The epithallus appears as a distinct layer of flattened cells (Pl. 2, Fig. 2) whose outermost walls are sometimes slightly rounded. Epithallial cells 10 μm in diameter and 4 mm long. Subepithallial initials are shorter than the cells immediately subtending them (Pl. 2, Fig. 2). Flattened multiporate sporangia conceptacles occur (Pl. 2, Fig. 1); in longitudinal section their shape is rectangular, with rounded lateral walls and flat roof. The available specimens supply no reliable data on both roof thickness and pores. At the time of their formation, conceptacles were raised only one half above the thallus surface. Their floor is usually 4–5 cell layer underneath the surrounding original plant surface. Since the conceptacles were scarcely protruding, growth rhythms of peripheral region (i.e. the so-called zonation) persist very regular not only in sterile but also in conceptacle-bearing portions. After burial, conceptacles chambers remain either empty or partially filled with bundles of elongated cells which are likely due to secondary growth of peripheral filaments inside old conceptacles (Pl. 2, Fig. 1). These neo-formations within buried conceptacles have been documented both in living (e.g. Basso 1996, Pl. 4, Fig. 4) and in fossil corallinaceans (Aguirre & Braga 1998, Pl. 3, Fig. 5).

Remarks

Phymatholiton sp.2 differs from *Phymatholiton* sp.1 mainly in having flattened conceptacles more sunken into thallus surface and, as a consequence, growth rhythms wide and regular instead of short and lenticular. Only few fragments referring to this species occur in the studied material. 'Lithothamnium sp. indet. A' from Monte Giglio (Beckmann et al. 1982) is similar in growth morphology, cell size and zonation but the features

of its conceptacles look somewhat different from those of *Phymatholithon* sp.2. Occurrence: thin sections Mto1B, Mto2A.

Genus *Mesophyllum* Lemoine 1928

Lectotype species: *Mesophyllum lichenoides* (Ellis) Lemoine 1928

Diagnostic features preservable in fossil material

Thallus nongeniculate, internal construction monomerous, presence of coaxial arrangement of core filaments, interfilamental cell fusions present, secondary pits absent, epithallus with flattened or rounded but not flared terminal cells, meristems with cells as long as or longer than their immediate inward derivatives, multiporate asexual conceptacles.

Remarks

Since Lemoine (1928) established this genus, a coaxial arrangement of core filaments has been for a long time regarded as diagnostic for *Mesophyllum* (Wray 1977). At present, some authors do not accept the validity of this feature and focus on spermatangial characters (which are unfortunately lacking in fossil potential), since the coaxial organisation of the ventral core has been shown to be somewhat variable, even within the same specimen (Woelkerling & Harvey 1993). In other terms, the occurrence of a coaxial core would not be a persistent character and consequently would not have a diagnostic value. However, among melobesioid genera, *Mesophyllum* is the only one always showing a coaxial core even if this may locally change to a non-coaxial one. Furthermore, the type species *Mesophyllum lichenoides* (Ellis) Lemoine exhibits a distinct coaxial core and all living Melobesioideae so far ascribed to *Mesophyllum* on the ground of the above-mentioned new criteria show a coaxial core. Therefore, in fossil melobesioids the presence of a distinct coaxial arrangement at least in some portions of the core can still be regarded as a key feature in delimiting the genus *Mesophyllum*. Fossil species of *Mesophyllum* have been separated by considering the same specific features as those described for the genus *Lithothamnion*.

Mesophyllum sp. 1
(Tab. 1; Pl. 2, Fig. 3–6)

Description

Plant with layered to foliose (Pl. 2, Fig. 3), less frequently warty, growth form. Thallus pseudoparenchymatous with dorsiventral organisation of monomerous type. The core and peripheral regions are strongly differentiated. Coaxial to non-coaxial cord-like ventral core up to 140 μm thick (Pl. 2, Fig. 4). Some core filaments weakly curve towards the substrate while other derivatives bend outwards and form a peripheral region with compact arrangement of small, squarish cells (Pl. 2, Fig.

4). Longer cells (11–20 μm, not recorded in Tab. 1) occur only in fertile portions of the thallus, beside the conceptacles, and are clearly related to their development (Pl. 2, Fig. 5). The peripheral region is well developed and commonly slightly zoned, each growth rhythm consisting of four to seven cell layers. This feature appears more evident in conceptacle-bearing portions, where irregular growth zones are present. Both in the ventral core and in the peripheral region, cells of adjacent filaments are connected side by side by fusions; these are especially evident in the long cells close to the conceptacles. The epithallus is one cell-layer thick (Pl. 2, Fig. 6). Its cells are 6–8 μm in diameter and 5–6 μm long; their shape is clearly flat to weakly rounded. Subepithallial initials could have been observed only within the roof of one conceptacle (Pl. 2, Fig. 6), where they seem virtually identical to the immediately underlying cells; however, it is worthy to be mentioned that roof filaments usually consist of cells whose shape is different from that visible in other portions of the thallus. Sporangia conceptacles multiporate, rectangular to elliptical in longitudinal section, with rounded lateral walls and a flat roof commonly composed of 4–5 cell layers; pore diameter 12–27 μm. Conceptacles compartments were originally protruding almost exactly one half above the surrounding thallus surface; their floor was 8–10 cells beneath the original plant surface. After burial, conceptacles remain either empty or completely filled with irregular net-like structures (Pl. 2, Fig. 5), which are possibly related to remains of spores. The renewal of the vegetative growth often left a cavity above the conceptacles; it appears approximately triangular, more or less flattened, and filled with sparry calcite (Pl. 2, Fig. 6).

Remarks

This species is the most abundant in the studied material, where it commonly forms rhodoliths in association with *Sporolithon* sp. 1. *Mesophyllum* sp.1 shows many affinities with *Mesophyllum roveretoi* Conti 1943 which shares with it a large number of features, particularly growth habit, core morphology, shape and size of the cells. However, according to Conti's original diagnosis (Conti 1943, p. 55), the conceptacle size seems to be somewhat different, since the asexual reproductive organs in the type material would be 330–350 μm (versus 320–500 μm) wide and 160–200 μm (versus 130–160 μm) high. On the other hand, taking into account Conti's drawings and photo (Conti 1943, Pls. VII–VIII), the height of the reproductive chambers seems to be smaller and more likely fluctuating between 130 and 160 μm. This observation agrees also with later records of *Mesophyllum roveretoi*, based on direct comparisons with the types of the species. Among these, as to conceptacles Mastrorilli (1968) indicates mean values of 150 μm (height) and 450 μm (diameter); these measures well fit the specimens described here. Therefore, *Mesophyllum* sp.1 might be identified as or closely related to *Mesophyllum roveretoi* Conti. However, only a re-documentation of this latter species, providing further modern key features, would permit a conclu-

sive assignment. Finally, none of the species from the Monte Giglio section (Beckmann et al. 1982) shows affinities with *Mesophyllum* sp.1. Occurrence: thin sections Mto3A, Mto3C, Mto3D.

Mesophyllum sp. 2
(Tab. 1; Pl. 3, Fig. 1–5)

Description

Plant with rarely warty and more commonly lumpy to fructicose growth form (Pl. 3, Fig. 1). Protuberances are up to 2.2 mm long and up to 1.6 mm in diameter; these outgrowths are always unbranched. The thallus is pseudoparenchymatous of monomerous type, with dorsiventral organisation in crustose portion and radial arrangement in protuberances. In the basal portions of the thallus a sturdy ventral core 120–200 μm thick continuously develops (Pl. 3, Fig. 1–2) showing a distinct coaxial arrangement of rectangular to trapezoidal cells. Conversely, the renewal of vegetative growth over small damaged portions of plant surface always starts developing a non-coaxial ('plumose') ventral core which overlies older peripheral filaments (Pl. 3, Fig. 1). Derivatives of the branched basal core filaments curve towards the substrate and bend outwards forming the peripheral region. In the longest protuberances, a central core of filaments ('medulla', Pl. 3, Fig. 3) is visible. Both the peripheral region of crustose portions and the medullary filaments of protuberances are characterized by a zonation due to the presence of small, thick-walled cells at the top of each zone (Pl. 3, Fig. 4). This feature becomes particularly evident in the medullary filaments of the best-developed protuberances. The number of cells forming each growth zone depends on its thickness: 6–9 (less frequently 4) layers of large cells are followed by 1–2 layers of small ones. The transition from large to small cells within each growth zone is very sudden; for this reason, two sets of data are given for the small (l,d) and for the large (L,D) cells separately (Tab. 1). Thickness of the growth zones and medium size of their cells seem to be closely related: thinner growth zones consist of cells smaller than thicker ones. In the best-developed protuberances, the central filaments curve towards the periphery, where they consist of 14–18 small, squarish cells ('cortex', Pl. 3, Fig. 3). Cell fusions are very evident throughout the thallus (Pl. 3, Fig. 4).). The poor state of preservation of both epithallial and meristematic cells prevents any reliable observation. The peripheral regions of crustose portions as well as the cortical filaments of protuberances contain sporangia conceptacles (Pl. 3, Fig. 5). These are multiporate, elliptical to roundish in longitudinal section; the roof is commonly composed of three thin cell layers. At the time of their development, the conceptacle floor usually had a depth of 5 cells and, consequently, the reproductive chambers emerged one half above the surrounding thallus surface. Conceptacles are partially to totally filled with irregular, very poorly defined, structures.

Remarks

This species abundantly occurs in the studied material, but always as small fragments. *Mesophyllum* sp.2 closely resembles the melobesioid alga from the Monte Giglio section described as '*Mesophyllum* cf. *pfenderae* (Lemoine)' (Beckmann et al. 1982) which, however, lacks some relevant taxonomic characters, such as the basal ventral core of cell filaments. *Mesophyllum* sp.2 might recall some other species ascribed to this genus and developing zoned protuberances, particularly *Mesophyllum varians* Lemoine 1934; unfortunately, Lemoine's diagnosis does not inform about many key features (including the reproductive organs) and, consequently, prevents any as far as possible sound comparison. Occurrence: thin sections Mto1C, Mto2A, Mto3A.

Family Sporolitaceae Verheij 1993
Subfamily Sporolithoideae Setchell 1943

Genus *Sporolithon* Heydrich 1897
Type-species: *Sporolithon ptychoides* Heydrich 1897

Diagnostic features preservable in fossil material

Thallus nongeniculate, internal construction monomerous, core filaments non-coaxial, interfilamental cell fusions and secondary pits present, epithallus with flattened and flared cells. Sporangia formed on single stalk cells, arranged in sori and separated one another by interspersed calcified filaments (paraphyses).

Remarks

Moussavian & Kuss (1990) demonstrated the priority of *Sporolithon* Heydrich 1897 over *Archaeolithothamnium* Rothpletz since this latter was not validly published. According to Verheij (1992, 1993), cell and sporangia sizes, widely used in the past, do not have conclusive taxonomic value at species level. Among the characters preservable in fossil material, also the number of filaments between sporangia, the number of cells in the paraphyses, the occurrence of a basal layer of elongated cells underlying the sporangia, the amount to which sori are raised above the surrounding thallus surface as well as the fate of the old sporangia (i.e. if they are flaked off or not) are at present regarded as important taxonomic criteria.

Sporolithon sp. 1
(Tab. 1; Pl. 4, Fig. 1–3)

Description

Growth form layered to foliose, with many layers horizontally arranged or irregularly superimposed one upon another (Pl. 4, Fig. 1). Each layer is usually 120–350 μm thick. The thallus is pseudoparenchymatous with dorsiventral organisation of monomerous type. Poorly developed, but always well distin-

guishable, non-coaxial ventral core 40–60 µm thick (Pl. 4, Fig. 2–3). Cells of the core filaments run parallel to the substrate, adapting to its irregularities, and later curve outwards forming the peripheral region. The longest cells occur in the basal part of the core. New ventral cores repeatedly arise from the uppermost surface of the peripheral filaments and expand over older thallus portions (Pl. 4, Fig. 2), allowing the plant to reach a lush development. The peripheral region is 80–200 µm thick in sterile parts but expands up to 300 µm in conceptacle-bearing portions. Cells of peripheral filaments are continuously arranged in wavy vertical alignment, with vertical cell walls much thicker than horizontal ones (Pl. 4, Fig. 2). These latter are usually so thin that, under a low magnification (e.g. Pl. 4, Fig. 2), cells look elongated, whereas they are small and squarish. Within each single thallus growth rhythms are absent. Cell fusions as well as epithallial cells are probably present but not clearly visible. Sporangia (Pl. 4, Fig. 3) are ellipsoidal in shape and arranged in rows (sori) usually rising one-half, or somewhat more, above the surrounding plant surface. Each sorus consists of 18–24 elements; 1–2 (3) paraphyses can be interspersed between adjacent sporangia, but these latter may also join side by side. Number of cells in the paraphyses ranging from five to six. Sori usually arise from a basal layer of cells longer (up to 16 µm) than the underlying ones (Pl. 4, Fig. 3). Each sporangium usually develops from a single, trapezoidal in shape, stalk cell which is horizontally aligned with the long cells belonging to the basal layer (Pl. 4, Fig. 3).

Remarks

This species is abundant in the studied material, where it forms rhodoliths usually in association with *Mesophyllum* sp. 1. Applying modern taxonomic concepts, in the last years some *Sporolithon* species have been described or re-documented. A large number of analogies can be drawn between *Sporolithon* sp.1 and '*Archaeolithothamnium* sp.1 Lemoine 1930' from the Paleocene of Austria, a species newly re-documented by Rasser & Piller (1994). However, this latter species seems to have smaller sori and, on the basis of the re-description, it is not clear enough whether these reproductive organs develop upon a distinct layer of elongated cells. *Sporolithon aschersoni* and *Sporolithon* cf. *aschersoni* (Schwager) Moussavian & Kuss recorded from the Italian Eocene (Bassi 1995, 1998), differ from the present form, among other things, especially in having much longer peripheral cells and sori formed on a higher basal layer. Even less affinities with *Sporolithon* sp.1 are those shown by such Lemoine's species from Algeria as *Sporolithon brevium*, *S. glangeaudi* and *S. liberum*, which have recently been re-described (Aguirre & Braga 1998). Rasser & Piller (1999) gave a thorough description of two *Sporolithon* species from the Austrian Eocene but both these species must be considered separated from the one described here; only *Sporolithon* sp.2 Rasser & Piller 1999 shows some structural resemblance with the species studied here but has longer peripheral cells and sporangia of different shape and size lacking

the basal layer of elongated cells. In all the diagnostic features, *Sporolithon* sp.1 recorded here strongly differs from *Sporolithon* sp.1 described recently by Bassi & Nebelsick (2000, Lower Oligocene of northern Slovenia). Lastly, from the Paleocene Monte Giglio section Beckmann et al. (1982) recorded three '*Archaelithothamnium*' species which, however, are distinctly different from *Sporolithon* sp.1. Occurrence: thin sections Mto3B, Mto3C, Mto3D.

Sporolithon sp. 2
(Tab. 1; Pl. 4, Fig. 4)

Description

Growth form probably encrusting. Ventral core non-coaxial; owing to the poor state of preservation of core filaments, the size of their cells is not measurable. Peripheral region with rectangular cells strongly arranged in horizontal rows, with vertical cell walls much thinner than horizontal ones (Pl. 1, Fig. 4). Cells of adjacent filaments are commonly joined by abundant fusions. Growth zones absent. Epithallial cells have not been recognized. Sporangia are usually bean-like in shape, less frequently ellipsoidal, and arranged in rows (sori) with up to 42 elements; number of filaments interspersed between adjacent sporangia ranging from one to three, exceptionally four. Three to four cells, up to 25 µm long, form each paraphysis. Sori usually arise from a basal layer of cells longer (30–34 µm) than the underlying ones (Pl. 4, Fig. 4). Single, poorly defined stalk cells sometimes occur at the base of the sporangia. At the stage of their development, sori were likely flush with the surrounding thallus surface; old sori have been later buried into the thallus.

Remarks

Only few fragments referring to this species occur in the studied material. Among all the species described in this paper, this is the most poorly preserved and lacks some relevant characters, such as those related to the growth morphology and to the structure of core filaments. On the one hand, this hinders a sound comparison with other *Sporolithon* fossil records; however, among the species already listed in connection with *Sporolithon* sp. 1, this form well compares with the accounts (Bassi 1995, 1998) of both *Sporolithon aschersoni* and *Sporolithon* cf. *aschersoni* from which it differs mainly in showing a somewhat higher basal cell layer (H 30–34 µm versus 20–28 µm). On the other hand, although it occurs as incomplete thalli, this species is differentiated well enough by its characters; it is clearly not related to *Sporolithon* sp.1, with which it shares the size (but not the shape) of sporangia but from which differs in other key features (such as the height of the basal layer underlying sori and the number and size of cells in the paraphyses). Among the three species reported from the Monte Giglio section (Beckmann et al. 1982), only that described as '*Archaeolithothamnium* cf. *gunteri* Johnson & Ferris' shows some affinities with *Sporolithon* sp.1 but seems to

differ from it at least in having sporangia of somewhat different shape and size. Occurrence: thin section Mto1A.

5. Concluding remarks

The results of the present work confirm the high-resolution power attainable taking into account, together with some traditional features widely used in the past, several characters with low fossilisation potential used in the delimitation of living species. Likely, the main outcome achieved here is linked to the possibility of considering, when working on well-preserved fossil material, such structural features as those related to the meristems and to the epithallus simply using a petrographic optical microscope instead of having to resort to SEM. This makes less difficult the taxonomic identification at genus level and, as a consequence, allows to consider relevant neophycological criteria as a more easily workable tool for future investigations (especially paleoenvironmental analyses). With respect to the algal assemblage reported from Monte Giglio section (Beckmann et al. 1982), which is similar in both age and geological setting to the Montorfano one, only some limited analogies can be drawn. Two species from Montorfano (*Lithothamnion* sp. and *Mesophyllum* sp. 2, both common throughout the sampled section) probably also occur in the Monte Giglio section, whereas *Phymatholithon* sp. 2 and *Sporolithon* sp. 2 (both only occasional) show some affinities with species from Monte Giglio but do not seem near enough to them to be considered co-specific. *Phymatholiton* sp.1 (rare), *Mesophyllum* sp.1 and *Sporolithon* sp.1 (both very common rhodolith-builder species) likely do not have relationship with any species reported from Monte Giglio. However, none of the twenty species of nongeniculate Corallinales from Monte Giglio, identified on the basis of traditional criteria, can definitely be compared with any taxon from Montorfano. On the one hand, this is due to the fact that the traditional taxonomy did not take into account some diagnostic features regarded now as of primary importance. On the other hand, it is worth mentioning that, in all likelihood, the Montorfano assemblage contains further species in addition to those described here. Unidentified, mostly sterile fragments might represent some of the forms from Monte Giglio; however, lacking key diagnostic features they cannot be limited within the framework of the modern taxonomy and have not been considered here.

Lastly, a key is presented here for the identification of the species discussed in this paper.

6. Identification key

1. Multiporate asexual conceptacles. Subfamily Melobesioidae
   1.1. Non-coaxial core filaments, terminal epithallial cells flattened and flared, subepithallial cells as long as or longer than cells immediately below. *Lithothamnion* **sp.**

   1.2. Non-coaxial core filaments, terminal epithallial cells flattened or roundish but never flared, subepithallial cells as short as or shorter than cells immediately below. Genus *Phymatholithon*
   1.2.1. Growth rhythms irregular, rectangular to roundish conceptacles (H max 102 μm, mean 99 μm) completely raised above the surrounding thallus surface, narrow ventral core cells (D 8–10 μm). *Phymatholiton* **sp. 1.**
   1.2.2. Growth rhythms regular, very flattened rectangular conceptacles (H max 72 μm, mean 68 μm) raised one half above the surrounding thallus surface, medium-sized ventral core cells (D 10–13 μm). *Phymatholiton* **sp. 2.**
   1.3. Predominantly coaxial core filaments. Genus *Mesophyllum*
   1.3.1. Growth form layered to foliose, mean conceptacle size D 414 × H 146 μm, conceptacle roof thickness 32–52 μm. Zonation of peripheral filaments usually slight, unless around conceptacles where it becomes very irregular. *Mesophyllum* **sp. 1.**
   1.3.2. Growth form warty to fructicose, mean conceptacle size D 278 × H 134 μm, conceptacle roof thickness 20–22 μm. Protuberances with marked and regular zonation of the central core with boundaries running between a row of low and thick-walled cells below (mean l 10 μm) and a row of much higher cells above (mean L 20 μm); distinct cortex made of squarish cell. *Mesophyllum* **sp. 2.**
2. Asexual conceptacles arranged in sori. Family Sporolithaceae
   2.1. Sori developing on a basal layer of cells up to 16 μm long, ellipsoidal sporangia nearly one half raised above the surrounding thallus surface, paraphyses made of 5–6 cells. Small, squarish peripheral cells (L 8–12 × D 8–10 μm) vertically aligned with scarce interfilamental cell fusions. *Sporolithon* **sp. 1.**
   2.2. Sori developing on a basal layer of cells up to 34 μm long, bean-like sporangia flush with the surrounding thallus surface, paraphyses made of 3–4 cells. Medium-sized, rectangular peripheral cells (L 12–18 × D 8–10 μm) horizontally aligned with abundant and conspicuous interfilamental cell fusions. *Sporolithon* **sp. 2.**

Plate 1

Fig. 1. Typical coating sequence in rhodoliths from the Montorfano quarry. Sample Mto3.

Fig. 2. *Lithothamnion* sp. Conceptacles-bearing wavy peripheral filaments making up a protuberance. Thin section Mto3A.

Fig. 3. *Lithothamnion* sp. Non-coaxial ventral core of cell filaments and transition to the peripheral region. (cf. text-Fig. 3.A.1). Thin section Mto3A.

Fig. 4. *Lithothamnion* sp. Peripheral region and one cell-layer thick epithallus (arrows) which has been preserved by the later overgrowth of a peyssonneliacean alga (PEY, with polygonal cells). Epithallial cells are clearly flattened and flared. Thin section Mto3A.

Fig. 5. *Lithothamnion* sp. Detail of Fig. 2, showing an asexual thallus with lenticular growth zones. Buried conceptacles are partially to totally filled with structures which might represent remains of sporangia (large arrow on the left) and re-crystallized interspersed filaments (medium-sized arrow). Also formations hanging from the roof are visible (small arrow); these are probably linked to the growth of bundles of calcite crystals after the spore release. Thin section Mto3A.

Fig. 6. *Phymatolithon* sp.1. Zoned protuberance with filled conceptacles. Thin section Mto1B.

Fig. 7. *Phymatolithon* sp.1. Peripheral region and one cell-layer thick epithallus (between arrows) immediately covered with a thin non-coaxial ventral core belonging to the same species. See text-Fig. 4 for a further description. Thin section Mto1A.

420 R. Stockar

1 | 5 mm

2 | 500 µm

3 | 50 µm

P_EY

4 | 50 µm

5 | 100 µm

6 | 100 µm

7 | 50 µm
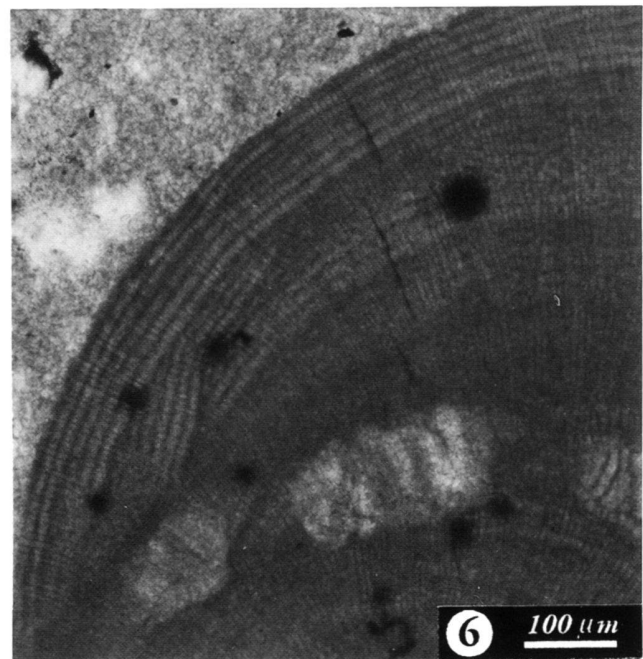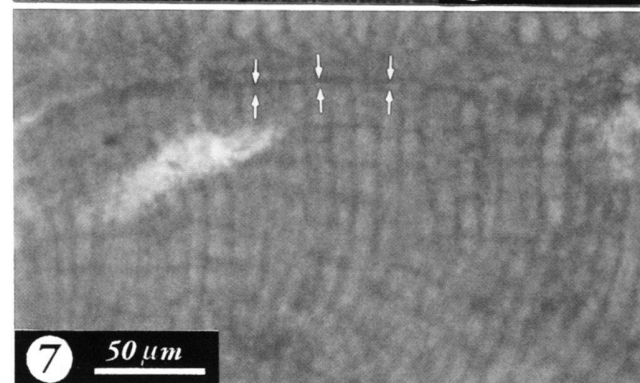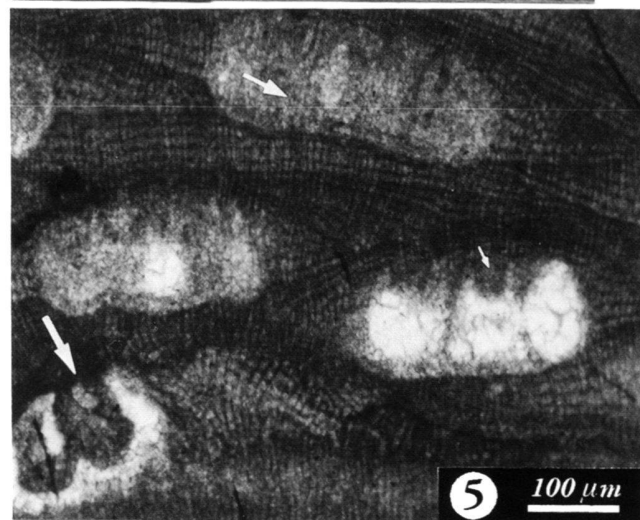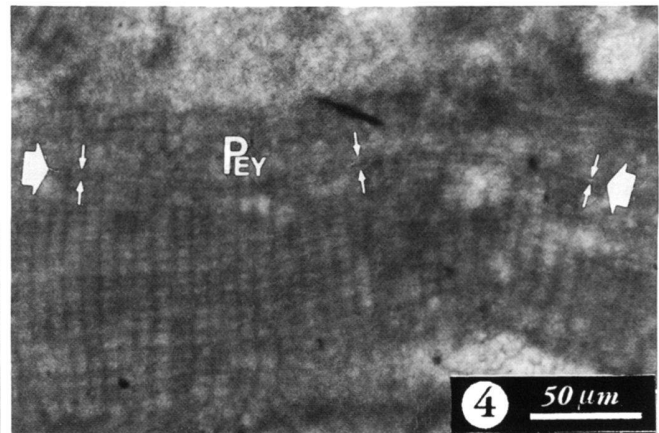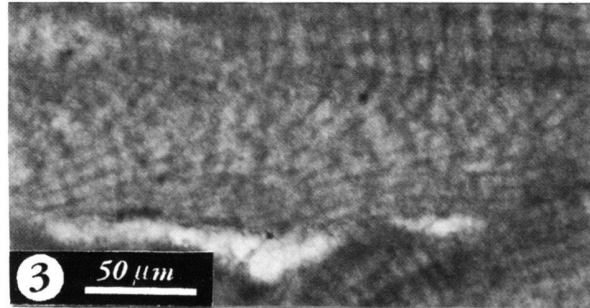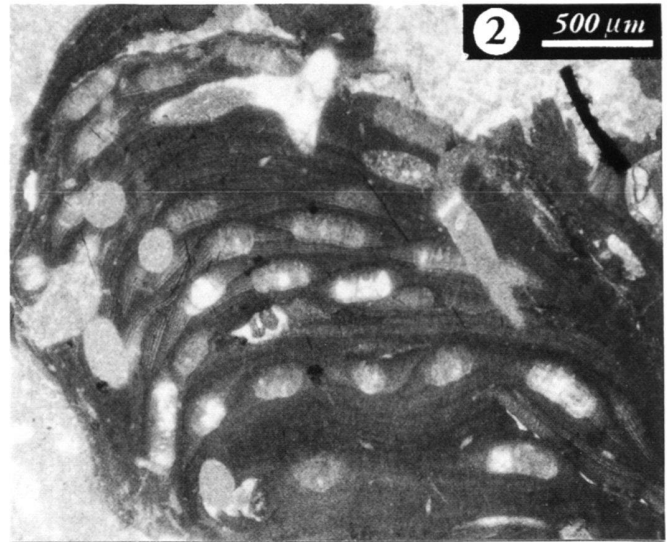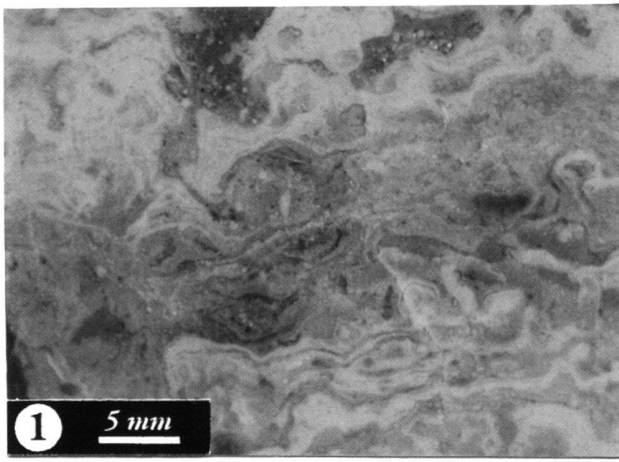
Plate 2

Fig. 1. *Phymatolithon* sp.2. Zoned peripheral region with flattened conceptacles. A bundle of elongated, very likely secondary, cell filaments is clearly visible within the right chamber (arrow). Thin section Mto1B.

Fig. 2. *Phymatolithon* sp.2. A single layer of flattened epithallial cells is clearly visible at the surface of the thallus (among the arrows). The subepithallial initials (sign +, as an example) are shorter than the underlying cells. Growth direction rightwards. Thin section Mto1B.

Fig. 3. *Mesophyllum* sp.1. Thallus with buried asexual multiporate conceptacles raised one half above the original plant surface. Thin section Mto3C.

Fig. 4. *Mesophyllum* sp.1. Coaxial ventral core of cell filaments (centre) and compact peripheral region (right). Growth direction rightwards. Thin section Mto3C.

Fig. 5. *Mesophyllum* sp.1. Detail of the long cells close to the conceptacles. The figured chambers are filled with irregular structures (possibly remains of spores). Thin section Mto3C.

Fig. 6. *Mesophyllum* sp.1. Detail of conceptacle roof structure. Cells forming the roof are crossed by pores (P) and covered with a well preserved epithallus (among the arrows). Above the conceptacle, the renewal of the vegetative growth left a flattened cavity, later filled with sparry calcite. Thin section Mto3D.
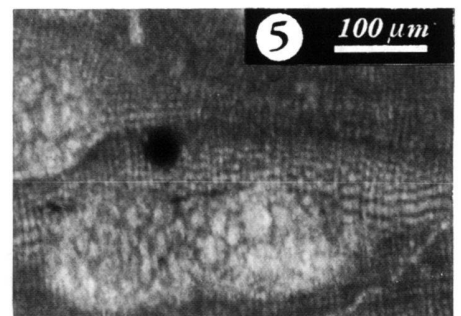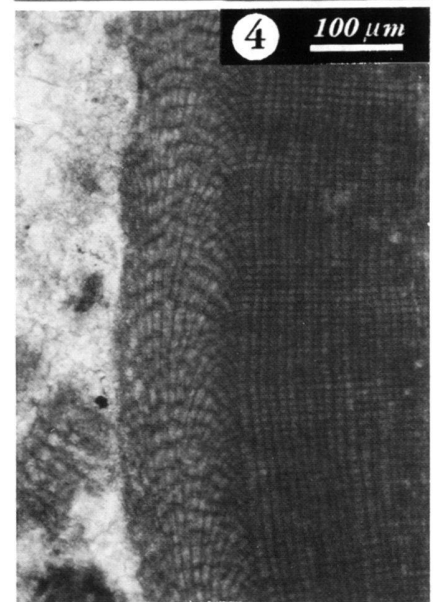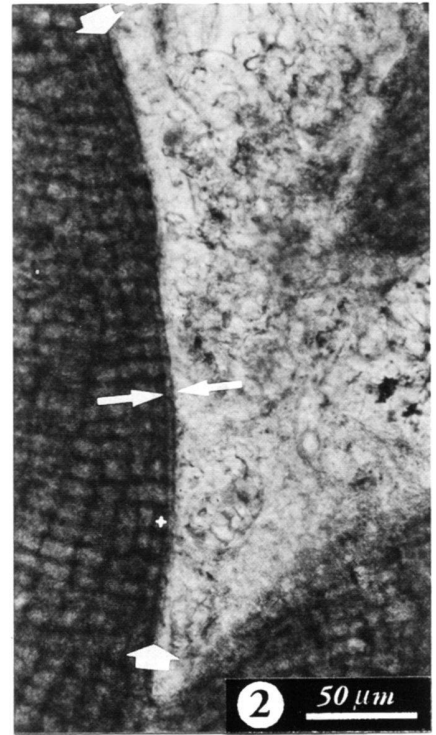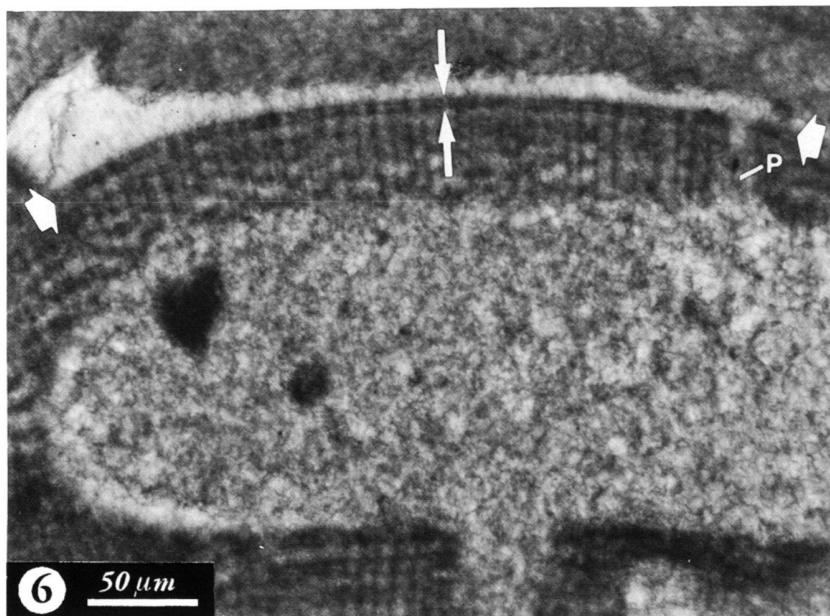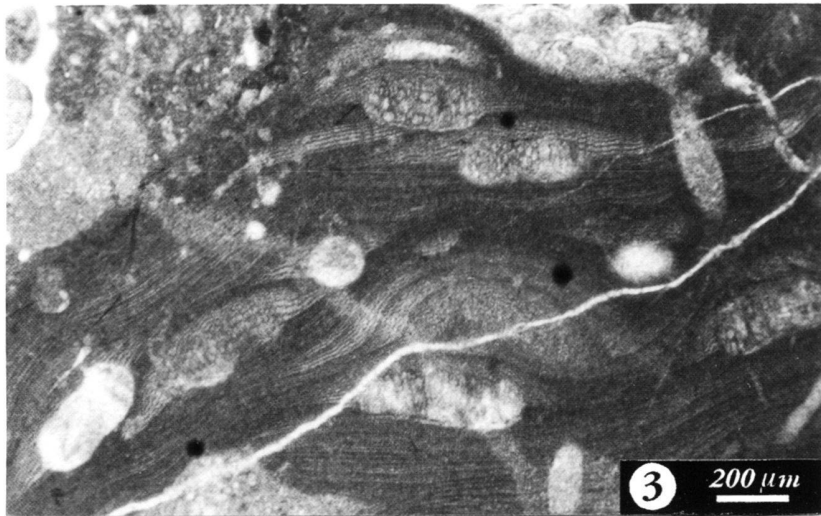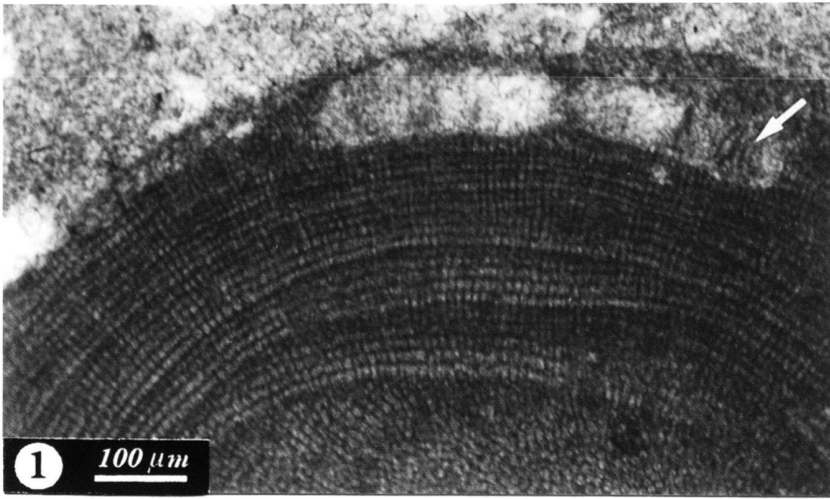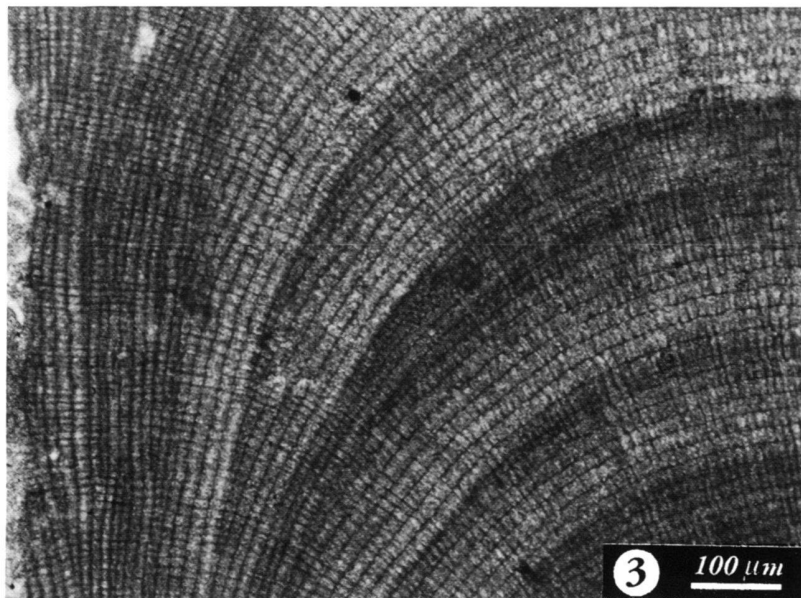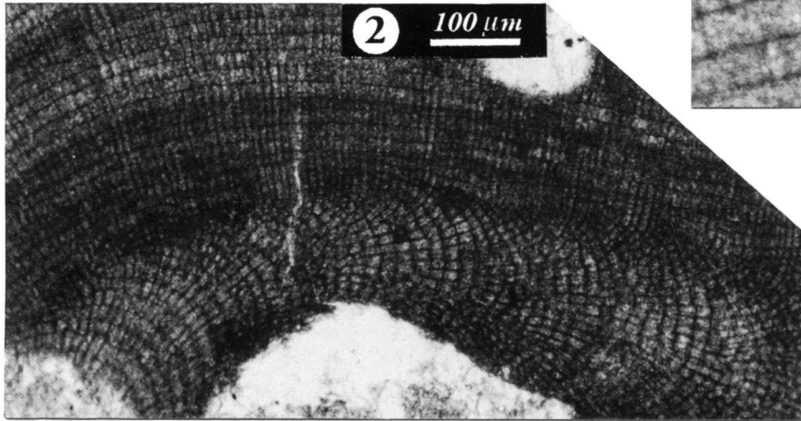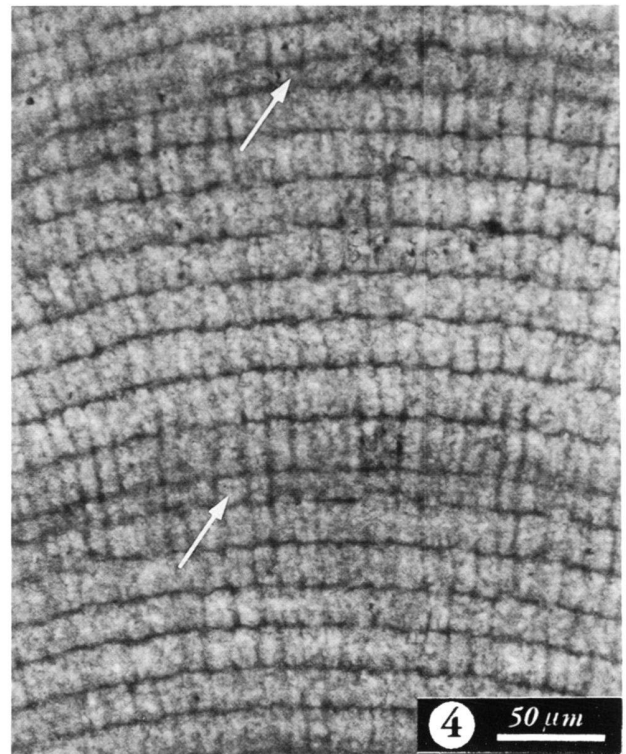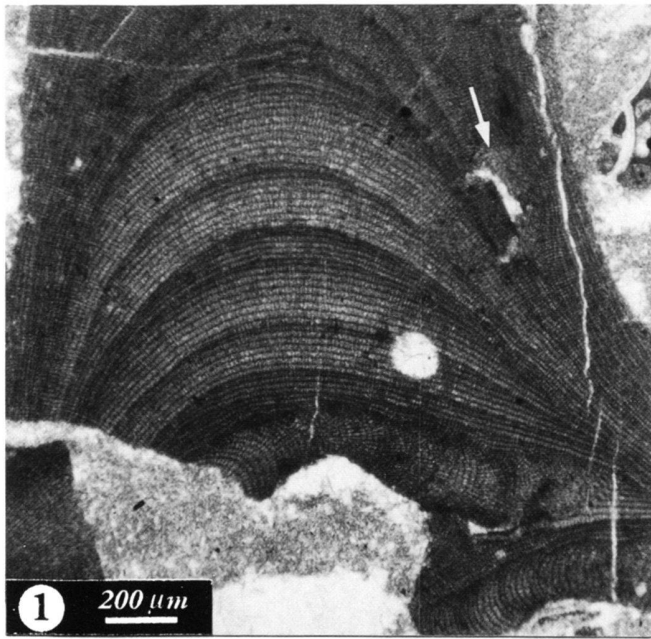
Plate 3

Fig. 1. *Mesophyllum* sp.2. Basal part of a protuberance. Note the co-existence of ventral cores with different arrangements. The basal ventral core (see also detail in Fig. 2) is coaxial while that overlying a small damaged area (arrow) develops with a non-coaxial ('plumose') organisation. Thin section Mto2A.

Fig. 2. *Mesophyllum* sp.2. Detail of Fig. 1 showing the basal ventral core with coaxially-arranged cell filaments. Thin section Mto2A.

Fig. 3. *Mesophyllum* sp.2. Detail of Fig. 1, showing the zoned central core of filaments ('medulla') diverging towards the periphery of the branch ('cortex', on the left). Thin section Mto2A.

Fig. 4. *Mesophyllum* sp.2. Detail of the central core of the filaments. Multiple cell fusions create a wide transversal connection between several horizontally aligned cells. The zonation is due to the presence of small cells at the top of each growth rhythm (arrows). Thin section Mto2A.

Fig. 5. *Mesophyllum* sp.2. Cortical filaments of a protuberance (on the right) bearing two multiporate conceptacles. Thin section Mto3A.
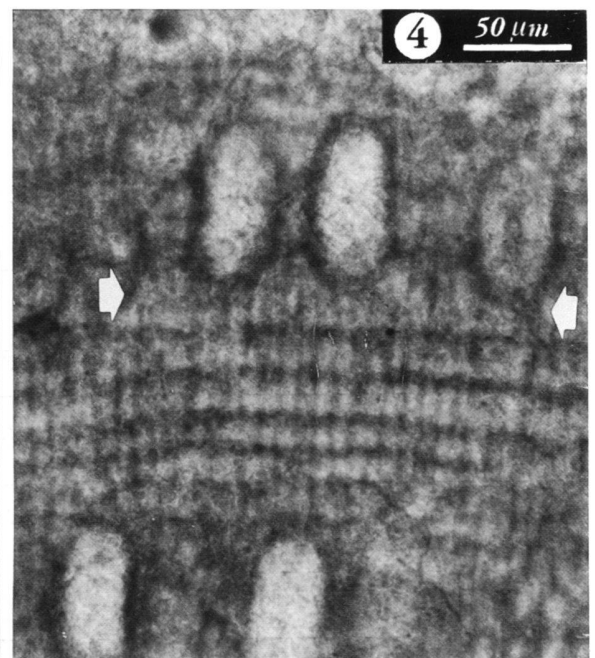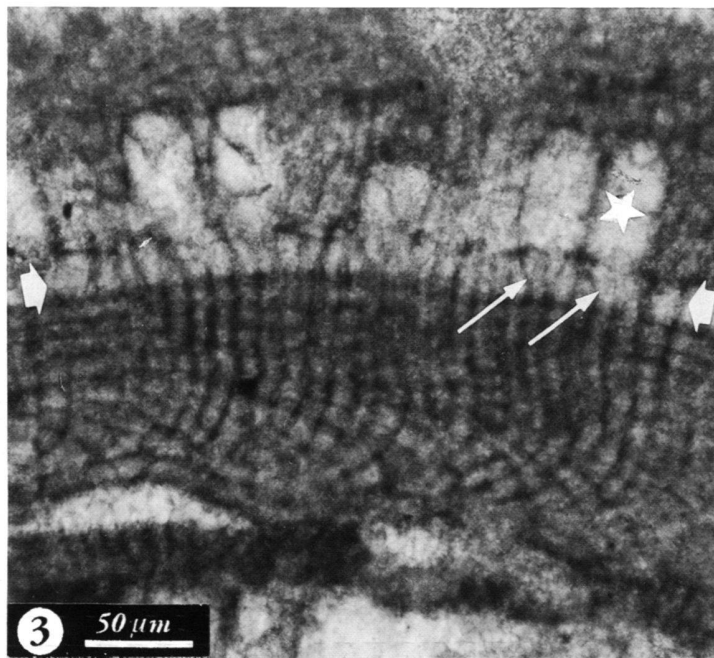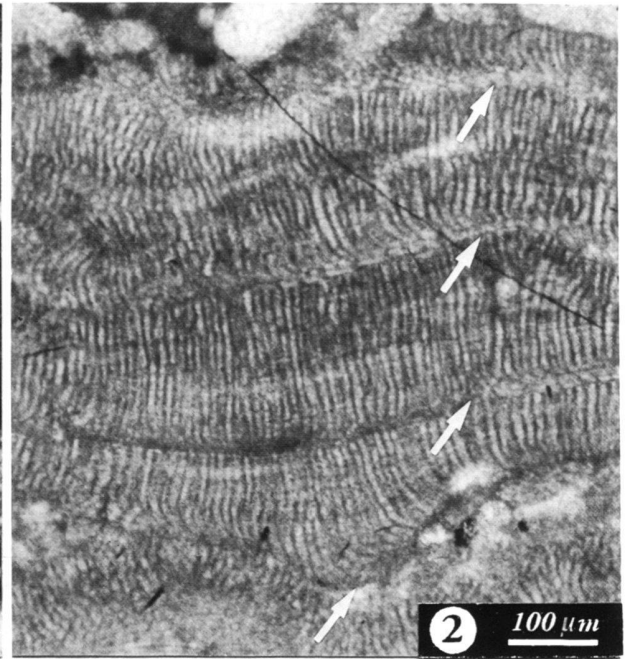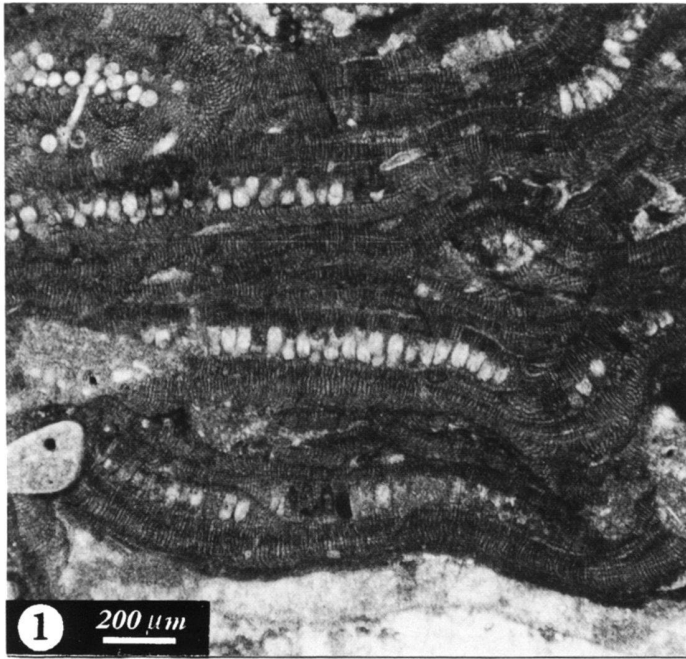
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Plate 4

Fig. 1. *Sporolithon* sp.1. Plant consisting of several thalli superimposed one upon another. Thin section Mto3C.

Fig. 2. *Sporolithon* sp.1. Superimposed sterile thalli showing poorly developed ventral cores (arrows) and vertical alignment in peripheral region. Thin section Mto3C.

Fig. 3. *Sporolithon* sp.1. Non-coaxial ('plumose') ventral core, peripheral region with squarish cells and sporangia (star) formed on a basal layer of elongated cells (between the large arrows). Basal stalk cells are also visible (e.g. long arrows, cf. text-Fig. 3.C.2). Thin section Mto3D.

Fig. 4. *Sporolithon* sp.2. Both cell layers below sporangia (between the arrows) and paraphyses consist of cells longer than those of *Sporolithon* sp. 1(Fig. 3). Cells of peripheral filaments, usually connected by abundant fusions, are rectangular and horizontally arranged. Thin section Mto1A.

REFERENCES

AGUIRRE J. & BRAGA J.C. 1998: Redescription of Lemoine's (1939) types of coralline algal species from Algeria. Palaeontology 41/3, 489–507.

AIROLDI M. 1932: Contributo allo studio delle Corallinacee del Terziario italiano. I: Le Corallinacee dell'Oligocene Ligure-Piemontese. Palaeontographia ital. 33, 55–83.

BASSI D. 1995: Sporolithon, Hydrolithon, Corallina and Halimeda in the Calcare di Nago (Eocene, Trento, Northern Italy). Ann. Univ. Ferrara 6/2, 11–25.

BASSI D. 1998: Coralline red algae (Corallinales, Rhodophyta) from the Upper Eocene Calcare di Nago (Lake Garda, Northern Italy). Ann. Univ. Ferrara 7, suppl., 1–50.

BASSI D. & NEBELSICK J.H. 2000: Calcareous algae from the Lower Oligocene Gornji Grad Beds of northern Slovenia. Riv. ital. Paleont. Stratigr. 106/1, 99–122.

BASSO D. 1995: Study of living calcareous algae by a paleontological approach: the non-geniculate corallinaceae (Rhodophyta) of the soft bottoms of the Tyrrhenian sea (Western Mediterranean). The genera Phymatolithon Foslie and Mesophyllum Lemoine. Riv. ital. Paleont. Stratigr. 100/4, 575–596.

– 1996: Living calcareous algae by a paleontological approach: the genus Lithothamnion Heydrich nom. cons. from the soft bottoms of the Tyrrhenian sea (Mediterranean). Riv. ital. Paleont. Stratigr. 101/3, 349–366.

BASSO D., FRAVEGA P., PIAZZA M. & VANNUCCI G. 1998: Revision and re-documentation of M. Airoldi's species of Mesophyllum from the Tertiary Piedmont Basin (NW Italy). Riv. ital. Paleont. Stratigr. 104/1, 85–94.

BECKMANN J.P., BOLLI H.M., KLEBOTH P. & PROTO DECIMA F. 1982: Micropaleontology and biostratigraphy of the Campanian to Paleocene of the Monte Giglio, Bergamo Province, Italy. Mem. Sci. geol., 35, 91–172.

BICHSEL M. 1977: Der Paleozänflysch des Montorfano Comasco: Sedimentation und Geröllinhalt. Unpubl. Thesis, Basel University, 68 p.

BOSENCE D.W.J. 1983: Description and Classification of Rhodoliths (Rhodoids, Rhodolites). In: PERYT T.M. (ed.), Coated Grains, Springer Verlag, Berlin, 217–224.

– 1991: Coralline Algae: Mineralisation, Taxonomy and Palaeoecology. In Riding R. (Ed.): Calcareous Algae and Stromatolites, Springer Verlag, Berlin, 98–113.

BRAGA J.C., BOSENCE D.J. & STENECK R.S. 1993: New anatomical characters in fossil coralline algae and their taxonomic implications. Palaeontology 36/3, 535–547.

BUXTORF A.& REICHEL M. 1936: Über das Alter der Lithothamnienkalke von Montorfano bei Como. Eclogae geol. Helv. 29/2, 497–499.

CABIOCH J. & GIRAUD G. 1986: Structural aspects of biomineralization in the coralline algae (calcified Rhodophyceae). In: LEADBEATER B. & RIDING R. (eds.): Biomineralisation in lower plants and animals. Systematic Ass., sp. vol. 30, Univ. Press Oxford, 141–156.

CONTI S. 1943: Contributo allo studio delle Corallinacee del terziario italiano. II: Le Corallinacee del Miocene del Bacino Ligure-Piemontese. Paleontographia ital. 41, 37–61.

HOTTINGER L. 1960: Recherches sur les Alvéolines du Paléocène et de l'Eocène. Schweiz. paläont. Abh., 75–76, 243 p.

KLEBOTH P. 1982: Stratigraphie und Sedimentologie der höheren Oberkreide und des Alttertiärs der Brianza (Provinz Como, Italien). Mem. Sci. geol. 35, 213–292.

LANTERNO E. 1958: Contribution à la connaissance de l'Eocène des environs de Varèse, de Côme et de Bergamo. Arch. Sc. (Genève) 11/2, 167–193.

LEMOINE M. 1928: Un noveau genre de Mélobésiées: Mesophyllum. Bull. Soc. bot. France 75, 251–254.

– 1930: Algues. In Kühn O. (Ed.): Das Danien der äusseren Klippenzone bei Wien. Geol. paläont. Abh. 17/5, 534–541.

– 1934: Algues calcaires de la Famille des Corallinacées recuillies dans le Carpathes occidentales par P. Andrusov. Verst. Serv. geol. Rep. Tchecoslov. 9/5, 269–285.

MASTRORILLI V.I. 1968: Nuovo contributo allo studio delle Corallinacee dell'Oligocene Ligure-Piemontese: i reperti della tavoletta Ponzone. Atti Ist. Geol. Univ. Genova, 5/2, 153–406.

MOUSSAVIAN E. & KUSS J. 1990: Typification and status of Lithothamnium aschersoni Schwager, 1883 (Corallinaceae, Rhodophyta) from Paleocene limestone of Egypt. A contribution to synonymy and priority of the genera Archaeolithothamnium Rothpletz and Sporolithon Heidrich. Berliner geowiss. Abh. Reihe A, Geol. Palaeont., 120/2, 929–942.

POIGNANT A.F. 1984: La notion de genre chez les algues fossiles. A. Les Corallinacées. Bull. Soc. géol. France 26, 603–604.

RASSER M. & PILLER W.E. 1994: Re-documentation of Paleocene coralline algae of Austria, described by Lemoine (1930). Beitr. Paläont. 19, 219–225.

– 1999: Application of neontological taxonomic concepts to Late Eocene coralline algae (Rhodophyta) of the Austrian Molasse Zone. J. Micropaleont. 18, 67–80.

SERRA-KIEL J., HOTTINGER L., CAUS E., DROBNE K., FERRANDEZ C., JAHURI A.K., LESS G., PAVLOVEC R., PIGNATTI J., SAMSÒ J.M., SCHAUB H., SIREL E., STRUOGO A., TAMBERAU Y., TOSQUELLA J. & ZAKREVSKAYA E. 1998: Larger Foraminiferal Biostratigraphy of the Tethyan Paleocene and Eocene. Bull. Soc. géol. France, 169/2, 281–299.

VERHEIJ E. 1992: Structure and reproduction of Sporolithon episoredion (Adey, Townsend et Boykins) comb. nov. (Corallinales, Rhodophyta) from the Spermonde Archipelago, Indonesia. Phycologia 31/6, 500–509.

– 1993: The genus Sporolithon (Sporolithaceae fam. nov., Corallinales, Rhodophyta) from the Spermonde Archipelago, Indonesia. Phycologia 32/3, 184–196.

WOELKERLING W.J. 1988: The coralline red algae: an analysis of the genera and subfamilies of non-geniculate Corallinacee. Oxford University Press, Oxford, 1–268.

WOELKERLING W.J. & HARVEY A. 1993: An account of southern Australian species of Mesophyllum (Corallinaceae, Rhodophyta). Phycologia 25/3, 379–396.

WOELKERLING W.J., IRVINE L.M. & HARVEY A. 1993: Growth-forms in Non-geniculate Coralline Red Algae (Corallinales, Rhodophyta). Austral. syst. Bot. 6, 277–293.

WRAY J.L. 1977: Calcareous Algae, Elsevier, Amsterdam, 1–185.