REASSESSMENT OF THE TYPE COLLECTIONS OF MASLOV’S SPECIES OF CORALLINALES (RHODOPHYTA). I. SPECIES ORIGINALLY ATTRIBUTED TO Lithophyllum AND Melobesia

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ABSTRACT

This paper is part of a wider project for reassessing Maslov’s original collection of fossil calcareous algae with a modern taxonomic approach. Based on this collection, currently housed in the Geological Institute of the Russian Academy of Sciences of Moscow, Maslov described many taxa of calcareous algae of diverse ages from the former USSR in two monographs and several other papers from 1929 to 1973. As in other taxonomic publications from those decades, many of Maslov’s new species of fossil coralline algae were distinguished by only a few characters of questionable taxonomic significance; in addition, most of his work was published in Russian with limited illustrations. This study deals in particular with Maslov’s original preserved material of species attributed by him to the genera Lithophyllum and Melobesia (Corallinales, Rhodophyta). Our reassessment indicates that only the types of Lithophyllum duplex Maslov, and Hydro lithon corculumis (Maslov) comb. nov. (= Lithophyllum corculumis) show significant features justifying their use as species names in coralline algal taxonomy. The type of Lithophyllum microsorum Maslov is a gametangial plant that cannot be compared with the tetrasporangial plants used to delimit other coralline algal species within the Corallinaeae subfamily Lithophyloideae. Although they are validly published species names, the lack of significant characters in the preserved types prevents any confident placement of “Melobesia (Lithoporella) badjii”, “Lithophyllum conocristatum”, “L. dioscurum”, “M. (L.) karpatica” “L. (Tenare?) lithothamnioides”, “L. pavlovii”, “L. platticarpum”, “L. premolucens var. cretacicum”, “L. senonicum”, “L. translucidum” in any defined generic or suprageneric taxon within the Corallinales. The holotypes of “M. (L.) parasitica” and “M. (Dermatolithon) ucrainicum” were not found and only thin sections later illustrated by Maslov are available.

Key words: calcareous algae, taxonomy, Maslov’s type collection, Corallinales, Rhodophyta.

RESUMEN

Este trabajo forma parte del proyecto de revisar con una perspectiva taxonómica moderna la colección de algas calcáreas fósiles de Maslov, depositada en el Instituto de Geología de la Academia de Ciencias de Rusia. Entre 1929 y 1973, Maslov describió muchos taxones de algas calcáreas fósiles, del Silúrico al Mioceno, de la antigua Unión Soviética, en dos amplias monografías y varios trabajos cortos. Como en otras publicaciones de aquellas décadas, muchos de sus nuevos taxones están basados en unos pocos caracteres de relevancia taxonómica discuti-
ble. Además, Maslov publicó la mayor parte de su trabajo en ruso y con exiguas ilustraciones. En concreto, este trabajo trata sobre los tipos de las especies que Maslov atribuyó a los géneros Lithophyllum y Melobesia. Sólo los tipos de Lithophyllum duplex Maslov y Hydroolithon corculumis (Maslov) comb. nov. (= Lithophyllum corculumis) presentan suficientes caracteres para ser usados como nombres de especies en la taxonomía de algas coralináceas. El tipo de Lithophyllum microsporum Maslov es una planta gametangial que no puede ser comparada con las plantas tetraesporangiales con las que se delimitan otras especies de Corallinaceae subfamilia Lithophylloideae. Aunque son nombres publicados válidamente, la ausencia de caracteres significativos en los tipos preservados impide asignar con seguridad “Melobesia (Lithoporella) badjii”, “Lithophyllum conocristatum”, “L. diascereusum”, “L. (L.) karpatica”, “L. (Tenarea?) lithothamniioides”, “L. pavlovii”, “L. platticarpum”, “L. premolucense var. cretaciculum”, “L. senonicum”, “L. translucidum” a ningún género o subfamilia de Corallinales. Los holotipos “M. (L.) parasitica” y “M. (Dermatolithon) ucrainicum” no se han encontrado y sólo se han podido estudiar ejemplares ilustrados posteriormente por Maslov.

Palabras clave: algas calcáreas, taxonomía, colección de tipos de Maslov, Corallinales, Rhodophyta.

INTRODUCTION

This paper is part of an attempt by researchers on fossil coralline algae to locate and reassess, using a modern taxonomic approach, the original collections of taxa of this algal group described during the 19th and first two-thirds of the 20th centuries (Rasser & Piller, 1994; Aguirre et al., 1996; Braga & Aguirre, 1998; Basso et al., 1998; Bassi et al., 2000; Woelkerling et al., 2002). Many species and genera of fossil coralline algae have been separated on the basis of only a few characters with slight or doubtful taxonomic significance. It is therefore imperative to restudy the original type material with new taxonomic perspectives to assess the status and circumscriptions of the taxa. As a consequence of the lack of reliable definitions, pre-existing names in the literature have not been commonly used by subsequent authors, who preferred to establish new species (and genera), further contributing to the large number of existing species names (Aguirre & Braga, 2005).

The ignorance or misunderstanding of previously established taxa was especially considerable in the case of the species described by Maslov, who published most of his work in Russian monographs, printed in the former USSR. Maslov described a large number of new taxa of fossil calcareous algae, most belonging to the Corallinales, from rocks originating in Silurian to Miocene sedimentary successions from the vast geographic area of the former USSR, from 1929 to 1973 (Bassi et al., 2002).

The first aim of this work is to reassess the type collections of species originally placed in Lithophyllum or Melobesia (Maslov, 1956, 1962; Maslov in Krivin & Maslov, 1962). No material has been found associated with two infraspecific names: Melobesia (Lithoporella) parasitica var. grandis Maslov, 1956 and Lithophyllum pavlovii var. irregularis Maslov, 1956. The second aim is to determine whether there is enough evidence in the preserved material to allow for placement of each taxon in a particular genus as delimited in a modern context. Assessing the relationships and the taxonomic status of species assignable to a particular genus is beyond the scope of the present study. This is the second contribution within the framework of the taxonomic revision of Maslov’s collection, after the reassessment of the corallinalean genera established by this author (Bassi et al., 2005).

MATERIAL AND METHODS

Maslov’s original material is represented by thin sections stored mostly in two boxes at the laboratory of palaeophycology in the Geological Institute of the Russian Academy of Sciences of Moscow. Examination of thin sections was carried out using light microscopy. Coralline-algal growth-form and anatomical terminology follows Woelkerling (1988), Braga et al. (1993), Woelkerling et al. (1993). Cell and conceptacle dimensions follow Chamberlain et al. (1988).

SYSTEMATIC PALAEOLOGY

ORDER CORALLINALES Silva & Johansen, 1986

The Corallinales is the only Order of Rhodophyta in which most or all vegetative cell walls are impregnated with calcite (Silva & Johansen, 1986). In the current taxonomy, three families with living representatives are recognized within the Corallinales: Corallinaceae, Hapalidaceae and Sporolithaceae (Harvey et al., 2003) (Tab. 1). The Solenoporaceae Pia, 1927 is traditionally regarded as an extinct family of coralline-like red algae, morphologically similar to but simpler than modern Corallinales, ranging from the Cambrian to the Palaeogene. However, the type-species of Solenopora is a chaetetid sponge (Riding, 2004) and the group also contains fossils resembling cyanobacteria as well as red algae (Braga & Riding, 2004). The families Corallinaceae and Hapalidaceae include four and three subfamilies, respectively (Tab 1). In contrast to current concepts of these taxa, Maslov (1956, 1962) included in the family Corallinaceae all modern corallinales...
and the ‘solenoporaceans’, and assigned all non-geniculate coralline red algae (‘solenoporaceans’ excluded) to the subfamily Melobesioideae (currently a subfamily within the Hapalidiaceae). Maslov (1956, 1962) included in *Lythophyllum* non-geniculate corallines with the following characters: encrusting, protuberant or branching plants; thallus consisting of cells well-arranged in rows; cell rows concentric in the “hypothallium” and parallel to the surface in the “perithallium”; conceptacle shape in vertical section like an inverted heart with a single pore at the top. He attributed to *Melobesia* Lamoroux, 1812 encrusting plants with one to two cell layers; “hypothallium” consisting of a single cell layer; and sporangial conceptacles, conical or hemispherical in shape, protruding on the thallus surface and possessing a single pore. In contrast to Maslov’s concept, in a modern context, *Lithophyllum* includes non-geniculate Lithophylloideae (see Tab. 1) with dorsiventral or bilateral (but not isobilateral) internal organization and lacking haustoria (Woelkerling *et al.*, 2002). Currently, *Melobesia* encompasses members of the subfamily Melobesioideae (Tab. 1), with a ventral unistratose layer of filaments and epithallial cells or multicellular filaments arising more or less perpendicularly from ventral-layer cells (dimerous construction) (Woelkerling, 1996).

**TAXA OF CERTAIN GENERIC PLACEMENTS**

The types of three of the species names established by Maslov (1962) and attributed by him to the genus *Lythophyllum* preserve vegetative and reproductive features that warrant their assignment to defined generic and suprageneric entities within the order Corallinales (Tab. 2). Two of them also permit their use in taxonomic work on fossil coralline algae.

**Family Corallinaceae** Lamouroux, 1812  
Subfamily Lithophylloideae Setchell, 1943  
Genus *Lithophyllum* Philippi, 1837

*Lithophyllum duplex* Maslov, 1962  
Figs. 2a-c

1962 *Lithophyllum duplex* Maslov, 82-83, pl. 21, figs. 1-3, text-fig. 60.  
1971 *Lithophyllum duplex* Maslov; Poignant, 1172, pl. 1.  
1972 *Lithophyllum duplex* Maslov; Orzag-Sperber & Poignant, 118.  
1973 *Lithophyllum duplex* Maslov; Orzag-Sperber, Poignant & Poisson, pl. 4, fig. 4.  
1982 *Lithophyllum* cfr. *duplex* Maslov; Fravega & Vannucci, fig. 10.  
1985 *Lithophyllum* cfr. *duplex* Maslov; Pisera, 105, pl. 20, fig. 4.  
1988 *Lithophyllum duplex* Maslov; Studencki, 39, pl. 13, fig. 1-2.  
1989 *Titanoderma duplex* (Maslov, 1962) nov. comb.; Pisera & Studencki, 202-203, pl. 11, figs. 6-7; pl. 12, fig. 3.

**Holotype:** Designated by Maslov (1962, p. 82), thin section 396, illustrated in pl. 21, figs. 2-3 and text-fig. 60.

**Age and locality:** Badenian (Tortonian in Maslov, 1962), quarry of the Sakhkamen factory, village Medobory, Ukraine.
Examination of the type collection: Only one thin section, labelled and numbered 396 (Fig. 1). A portion of the plant illustrated by Maslov (1962) is marked by an ink circle.

This is a plant with successive growth phases or several superimposed plants with encrusting ventral portions that give rise to lumpy protuberances (at least 3 mm high) bearing numerous buried conceptacles.

The thallus construction is dimerous in the ventral region and monomerous in the protuberances. Cells at the ventral primigenious filaments are 10-15 μm in length and 17-22 μm in height. Postigenous filaments arise perpendicularly to the primigenous ones and then expand and arch upwards, becoming radially arranged in the protuberances. Cell filaments are clearly distinct suggesting that cells of adjacent filaments are only connected by secondary pits. Cells are rectangular in section and their size ranges from 10 to 16 μm in diameter and from 25 to 30 μm in length. Postigenous cells are slightly longer in the centre of protuberances. Lateral alignment of cells in adjacent filaments is well defined.

The numerous conceptacles (17), up 250 μm in diameter and up 120 μm in height, are uniporate and ellipsoidal in longitudinal section with a flat floor; they were sunken and became buried in the thallus. The pore canal is a funnel-like inverted cone. When new filaments cover the pore, the wider upper part of the pore remains as a small, second chamber on top of the conceptacle. These conceptacles could be either tetrasporangial or female/carposporangial.

Remarks: L. duplex has been illustrated only in a few cases although it is a typical component of rhodoliths in Mediterranean Neogene deposits (Fravega & Vannucci, 1987) and has been mentioned in several reports (Mastrorilli, 1968; Orszag-Sperber & Poignant, 1972; Orszag-Sperber et al., 1977; Fravega & Vannucci, 1982; Fravega et al., 1984). The specimen illustrated by Fravega & Vannucci (1982) was doubtfully assigned to L. duplex by the authors. The vegetative characters and the shape and size of the sporangial conceptacles of the depicted examples attributed by Pisera (1985), Studencki (1988) and Pisera & Studencki (1989) to this species are similar to those of the holotype. The latter authors doubtfully transferred L. duplex to Titanoderma Nägeli, 1858. The transfer was based upon the presence of a “unistratose hypothallus” both in the holotype and in plants from the Miocene of Poland. However, unistratose ventral primigenious filaments are common in Lithophyllum plants with dimerous construction and, therefore, the transfer of L. duplex to Titanoderma is not justified. In addition, Titanoderma Nägeli can be considered a younger synonym of Lithophyllum according to some authors (Campbell & Woelkerling, 1990; Woelkerling & Campbell, 1992). Even if Titanoderma is maintained as a separate entity it can only be distinguished from

**Lithophyllum** by the occurrence of a bistratose margin with oblique, palisade hypothallial cells in juvenile and regenerating plants (Chamberlain, 1991). Neither the holotype nor the Middle Miocene Polish examples display any of these features. Instead they possess thick peripheral regions comprising postigenous filaments made up of many cells, similar to those in *L. incrustans* Philippi, the type species of the genus. If the preserved conceptacle were tetrasporangial, their features (shape, size, shape of pore canal, etc) might be diagnostic characters in separating *L. duplex* from other *Lithophyllum* species; however, a discussion of the relationship of *L. duplex* to other congeneric taxa is beyond the scope of this work.

**Lithophyllum microsporum** Maslov, 1962

Figs. 2d-e

1962 Lithophyllum microsporum Maslov, 85-86, pl. 18, fig. 3, text-fieg. 63.

? 1972 Lithophyllum microsporum; Orsag-Sperber & Poignant, pl. 3, fig. 4.

? 1977 Lithophyllum microsporum; Orsag-Sperber, Poignant & Poisson, pl. 3, fig. 2; pl. 4, fig. 3.

? 1980 Lithophyllum microsporum Maslov; Vannucci, pl. 2, fig. 1.

? 1988 Lithophyllum microsporum Maslov; Studencki, 42, text-fig. 8.

1996 Lithophyllum microsporum Maslov; Basso, Fravega & Vannucci, 286-287, pl. 67, figs. 1-5 (holotype).

Holotype: Maslov (1962, p. 85) designated the sample 387/2 as the holotype. There are two thin sections with this numbering: 387/2 and 387/2u (Fig. 1). The first one is labelled “holotype”, probably by a curator of Maslov’s collection but the plant illustrated by Maslov (1962: pl. 18, fig. 3) is in thin section 387/2u. The latter was studied and illustrated as the holotype of *L. microsporum* by Basso et al. (1996). The two thin sections contain plants with similar vegetative characters and were most probably cut from the same hand sample. They can therefore be considered as two preparations from the holotype sample. Thin section 387/2, however, also contains specimens of coralline algae that are not conspecific with the ones in 387/2u.

Age and locality: Badenian (Tortonian in Maslov, 1962), village Staraj Sbarazh, western Ukraine.

Examination of the type material: The two thin sections (Fig.1) contain fragments of protuberances from one or several plants. Each fragment consists of a single system of dividing, fan-like cell filaments. Changes in the density (darkness) of micrite in the cell walls depict weak growth zonation. Well-defined cell walls separating adjacent filaments clearly indicate the absence of cell fusions and suggest that only secondary pits connect adjoining cells (7-10 μm in diameter and 16-20 μm in height). The numerous preserved conceptacles are small (70-86 μm in diameter and 32-38 μm in height) and flat-elliptical in longitudinal section. The pore canal is large relative to the size of the conceptacle chamber and conical in shape. In several cases the chamber, together with the pore, is triangular in section. The size and shape of the conceptacle in the type of *L. microsporum* are typical of gametangial, particularly spermatangial, conceptacles of members of the subfamily Lithophylloideae.

Remarks: The vegetative features of the protuberance fragments in the holotype of *L. microsporum* are diagnostic of *Lithophyllum* (Lithophylloideae, Corallinaceae). The characters supposedly separating this from other *Litho-

**L. microsporum**$^*$

...
The occurrence of cell fusions in the thalli with dimerous construction would suggest an affinity of *Melobesia* (L.) type belongs to the well-characterized species to which, therefore, the name can be applied.

*Melobesia* (*Lithoporella*) *badjii* Maslov, 1956

Figure 3. *Melobesia* (*Lithoporella*) *badjii* Maslov, 1956. Many superimposed thin encrusting plants or superimposed applanate branches of one or several plants with dorsiventral dimerous thalli.

**Description**: The remaining thin section (numbered 7/3) contains the plant or plants described and illustrated by Maslov (1962: pl. 69, fig. 1) (Fig. 1). There are many superimposed thin, encrusting plants or superimposed applanate branches of one or several plants (230 μm thick) that grew on a bioclast. The original calcite in the cell walls seems to be recrystallized and the plants are poorly preserved. Thalli are dorsiventral with dimerous construction. Cells in primigenous filaments are connected by cell fusions. Small flattened cells locally preserved on top of the primigenous ones can be interpreted as epithallial cells that formed the very short postigenous filaments. No conceptacles can be recognised.

**Remarks**: The occurrence of cell fusions in the thalli with dimerous construction would suggest an affinity of *M. (L.)*
badjii with genera in the Corallinaceae subfamily Mastophoroideae or the Hapalidiaceae subfamily Melobesioidae, which show similar vegetative features. In the Mastophoroideae, species in genera such as *Hydrolithon* Foslie, 1909, *Lithoporella* Foslie, 1909, *Mastophora* Decaisne, 1842 and *Pneophyllum* Kützing, 1843 have dimerous thalli 2-3 cells thick and uniporate sporangial conceptacles (Woelkerling, 1996). The genus *Melobesia* Lamouroux, 1812 (Melobesioidae) has similar vegetative features with multiporate sporangial conceptacles (Woelkerling, 1988, 1996). The absence of any reproductive structure in the plants in the type of *M. (L.) badjii* prevents any reliable assignment of the species to precise generic and suprageneric taxa within the Corallinales (Tab. 2).

**Lithophyllum conocristatum** Maslov, 1962

Figs. 4a-b

1962 *Lithophyllum conocristatum* Maslov in Krivin & Maslov, 69-70, text-fig. 5.

**Maslov’s disposition**

Family Corallinaceae

Subfamily Melobesioideae

**Disposition proposed in this paper**

Order **CORALLINALES**

Silva & Johansen, 1986

Family **Corallinaceae**

Lamouroux, 1812

*Lithophyllum duplex* Maslov, 1962

*Lithophyllum corculumis* Maslov, 1962

*Lithophyllum microsporum* Maslov, 1962

*Lithophyllum premoluccense* var. *cretacicum* Maslov, 1956

*Lithophyllum platticarpum* Maslov, 1962

*Lithophyllum dioscurensum* Maslov, 1956

*Lithophyllum conocristatum* Maslov in Krivin and Maslov, 1962

*Lithophyllum (tenarea?!) lithothamnioides* Maslov, 1962

*Lithophyllum pavlovii* Maslov, 1956

*Lithophyllum senonicum* Maslov, 1956

*Lithophyllum translucidum* Maslov, 1956

*Melobesia* (*Lithoporella*) *badjii* Maslov, 1956

*Melobesia* (*Lithoporella*) *karpatica* Maslov, 1962

*Melobesia* (*Lithoporella*) *parasitica* Maslov, 1956

**Holotype:** Designated by Maslov in Krivin & Maslov (1962, p. 70), thin section 15/59 (now labelled as 15/5).

**Age and locality:** Danian, Zayachusskaya formation, Eastern Carpathians, Rakhovsky district, village Kobyletzhskaya poliana, Shopurka river valley, Ukraine.

**Examination of the type material:** The only remaining type material is the holotype thin section (Fig. 1). It contains two branches of a plant or two plants growing one over the other. The thallus is encrusting, dorsiventral and monomerous. Cell filaments run parallel to the substrate forming a plumose ventral core and curve upwards to become perpendicular to the dorsal surface. Cell fusions are frequent in adjacent filaments. Cells are generally small, slightly larger in the core than in the peripheral region (4-6 μm in diameter and 6-10 μm in height).

The only preserved conceptacle protrudes conspicuously on the thallus surface. It is uniporate and trapezoidal in section, 330 μm in diameter and 130 μm in height. The pore canal is cylindrical (62 μm in diameter) to slightly conical and relatively long (143 μm). The filaments of the conceptacle roof around the pore are arranged in fans oblique to the pore walls. There

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**Table 2.** Summary of the proposed taxonomic disposition of the studied species.
are no remaining characters to aid in discerning whether it was a gametangial or a sporangial conceptacle.

**Remarks:** The uncertain nature of the preserved conceptacle prevents the assignment of the type of *L. conocristatum* to a precise family and subfamily within the Corallinales (Tab. 2). If it were a gametangial conceptacle, its size would suggest that the type belongs to a genus of Melobesioideae within the family Hapalidiaceae (see Harvey et al., 2003), such as *Lithothamnion* or *Phymatolithon*. If the conceptacle were a sporangial one, the species would have to be included in the *Corallinales* subfamily Mastophoroideae, most probably in the genus *Spongites*.

***Lithophyllum dioscurensum*** Maslov, 1956  
Figs. 4c-d

1956 *Lithophyllum dioscurensum* Maslov, 120, pl. 34, fig. 8, text-fig. 50.  
1962 *Lithophyllum dioscurensum* Maslov; Maslov, 81-82, text-fig. 59.

**Holotype:** Designated by Maslov (1956, p. 129), thin section 3504/5037, now numbered 5037c/2.

**Age and locality:** Danian?, Iora river basin, Georgia.

**Examination of the type material:** The thin section (Fig. 1) contains a large fragment of a long protuberance, about 2 mm long and 0.5 mm in diameter. It consists of a single system of radiating and dividing cell filaments, arranged in a fan-like pattern. The primary cell walls of cells in adjacent filaments are laterally well aligned, generating the coaxial structure of the protuberance core. Cells are generally small (7-10 μm x 12.5-20 μm) and slightly longer in the centre of the coaxial core. Cell fusions are common, especially in the outer region of the protuberance.

Two structures preserved in the outer region of the plant can be interpreted as the remains of the early developmental stages of two multiporate conceptacles, up to 150 μm in diameter and 40 μm in height (Fig. 4c-d). The poorly defined long cells in these structures probably reflect cell elongation of conceptacle primordia, which takes place within the thallus in many coralline species (Aden, 1965; Woelkerling, 1988).

**Remarks:** The co-occurrence of cell fusions and multiporate conceptacles in the holotype of *L. dioscurensum* indicates that the plant belongs to the Hapalidiaceae subfamily Melobesioideae. The absence of further diagnostic characters prevents any confident assignment of the species to a definite genus within this subfamily (Tabs. 1, 2).

***Melobesia (Lithoporella) karpatica***  
Maslov, 1962  
Figs. 4e-f

1962 *Melobesia (Lithoporella) karpatica* Maslov, 99-100, pl. 24, fig. 3, text-fig. 78.

**Holotype:** Designated by Maslov (1962, p. 100), thin section 249, illustrated in pl. 24, fig. 3, text-fig. 78.

**Age and locality:** Palaeogene, village Strelbichi, pre-Carpathians.

**Examination of the type material:** The analysed thin section contains the specimen described and illustrated by Maslov (1962, pl. 24, fig. 3) (Fig. 1). It is a broken, thin encrusting thallus, 5 mm long and 0.12 mm thick, cut with changing orientation in the section. The thallus is dorsiventral and dimerous. Primigenous cell filaments are composed of palisade cells (17-18 μm in diameter and 22-26 μm in length) connected by cell fusions. The short postigenous cell filaments consist of several cells (13-17 μm in diameter and 17-20 μm in length) connected by cell fusions. The outer thallus surface is badly preserved and no possible epithallial cells can be recognised. No reproductive structures can be observed in the holotype.

**Remarks:** The vegetative characters (fusions of cells of adjacent filaments) of the holotype suggest an affinity of *M. (L.) karpatica* with genera in the *Corallinales* subfamily Mastophoroideae or in the Hapalidiaceae subfamily Melobesioideae. The absence of any reproductive structures in the plants in the type of *M. (L.) karpatica* prevents any reliable assignment of the species to particular generic and suprageneric taxa within the *Corallinales* (Tab. 2).

***Lithophyllum (Tenarea?) lithothamnioides***  
Maslov, 1962  
Figs. 5a-b

1962 *Lithophyllum (Tenarea?) lithothamnioides* Maslov, 96-97, pl. 27, fig. 3, text-fig. 75.  
? 1988 *Lithophyllum lithothamnioides* Maslov; Studencki, 40, pl. 7, fig. 3; pl. 14, figs. 1-2.  
? 1989 *Lithophyllum lithothamnioides* Maslov; Pisera & Studencki, 201, pl. 11, fig. 1.

**Lectotype:** Maslov (1962, p. 96) designated the thin section 1047 as the ‘holotype’ but all the illustrations he provided of the species correspond to thin section 1048. The latter is not an additional preparation from the same hand sample but from a different one. According to ICBN Article 9.13 (Greuter et al., 2000), “The holotype (or lectotype) of a name of a species or infraspecific taxon of fossil plants is the specimen (or one of the specimens) on which the validating illustrations are based. When… in the protologue of a name of a new taxon… a type specimen is indicated but not identified among the validating illustrations a lectotype must be designated from among the specimens illustrated...”. In accordance with this article, we herein select as the lectotype the plant in thin section 1048 (Fig. 1; Fig. 5a-b), which is the only one illustrated by Maslov (1962: pl. 27, fig. 3 and text-fig. 75) when he established *Lithophyllum (Tenarea?) lithothamnioides*. It is a branching, laminar plant, a portion of which is marked with an ink circle by the Russian author (Fig. 5a).

**Age and location:** Badenian (Tortonian in Maslov, 1962), Tarkhankut peninsula, Crimea.
Examination of the type material: There are two thin sections from Maslov’s original collection of *L. (T.?) lithothamnioides*: the one containing the lectotype designated here and the one (invalidly) designated as the ‘holotype’ (Fig. 1). The two thin sections contain contorted and branching laminar plants several millimetres in length and about 0.15 mm in thickness, which grew on a soft, fine-grained substrate. The thalli are monomorphic with bilateral growth: a single system of radiating filaments that grew and curved outwards to both sides, although one direction may be preferential in portions of the thalli. Due to contortion, branching and random orientation of the different plants in the fine-grained matrix of the rock, it is difficult to recognise the polarity of plant growth. Cells of adjacent filaments are frequently fused; cell walls are not laterally well aligned. Cells in the core of the thalli are long and become shorter towards the outer surfaces (7-10 μm in diameter and 16-20 μm in height). Flat cells that can be interpreted as epithallial cells (10-20 x 5 μm) are locally preserved at the filament tips, forming a laterally continuous layer. They have lighter calcite walls, a feature common in present-day and fossil epithallial cells. These rows of epithallial cells were interpreted by Maslov (1962) as thin crusts of *Melobesia parasitica* Maslov (see below). However, as stated by Studencki (1988), each flat cell is the terminal cell of a subtending filament in the thallus.

No conceptacles were observed in the preserved type material.

Remarks: Maslov (1962) doubtfully attributed this species to *Tenarea* Bory, 1832, as a subgenus of *Lithophyllum* Phillipi, 1837, probably due to the bilateral orientation of the cell filaments in the thalli. As pointed out by Woelkerling (1988), *Tenarea* has undergone marked changes in its circumscription since its description but according to a modern revision of the type species (Woelkerling et al., 1985), *Tenarea* is readily differentiated from other coralline algal genera. It has an isobilateral organisation with two central rows of primigenous filaments of palisade cells that is unique among the known coralline algae. As in other lithophyllid genera, cells of adjacent filaments in *Tenarea* are joined by secondary pits with no cell fusions.

The occurrence of cell fusions in the type of *lithothamnioides* suggests that it belongs either to the subfamily Melobesioideae in the family Hapalidiaceae or to the subfamily Mastophoroideae in the Corallinaceae. The lack of sporangial conceptacles and other diagnostic characters, however, prevents any confident attribution of the species to any taxon at the generic or subfamily levels (Tab. 2). The plants illustrated by Studencki (1988) in pl. 7 fig. 3 (bottom) and pl. 14 fig. 1 might be conspecific with the *lithothamnioides* lectotype, but the lack of diagnostic features prevents any confident comparison. As stated by Studencki (1988, p. 40), it is very difficult to recognise whether the conceptacle in the plant in pl. 14 fig. 2 in Studencki (1988) occurs within a thallus similar to the *lithothamnioides* lectotype or whether it belongs to a different plant. In addition, no features distinctive of *lithothamnioides* can be observed in the thallus with a possible conceptacle illustrated (but not described) by Pisera & Studencki (1989, pl. 11, fig. 1). The specific circumscription of these latter two specimens remains uncertain and consequently no conceptacles have been confidently recognised in plants attributable to “*L. lithothamnioides*” Maslov.

**Lithophyllum pavlovii** Maslov, 1956

![Figure 5c](image)

1956 *Lithophyllum Pavlovii* Maslov, 120-121, pl. 34, figs. 2 and 4, text-fig. 51.

1962 *Lithophyllum pavlovii* Maslov; Maslov, 86-87, text-fig. 64.

Holotype: Designated by Maslov (1956, p. 120), thin section 3504/110 (Fig. 1), illustrated in pl. 34, figs. 2 and 4 and text-fig. 51. In addition to the illustrated specimen, there are other coralline algal fragments in the thin section that might be conspecific.

Age and locality: Danian?, Iora river basin, Georgia.

Examination of the type material: The plant illustrated by Maslov is a small, isolated fragment (1.5 x 0.5 mm in size) that consists of a single system of radiating and dividing, fan-like arranged filaments. It is difficult to determine whether it represents a branch fragment of a nongeniculate or an intergeniculate segment of a geniculate coralline.

Primary cell walls are laterally well-aligned in the core of the thallus, generating coaxial organisation; the cells are 5-10 μm in diameter and 22-25 μm in height. Cell filaments arch outwards to become perpendicular to the outer surface. Fusions of cells of adjoining filaments can be observed in longitudinal and transverse sections of filaments. No conceptacles are observed.

Remarks: The lack of diagnostic characters in the type of the species prevents its assignment to known genera or subfamilies within the Corallinales (Tab. 2). If this were a geniculate coralline, the occurrence of cell fusions would suggest an affinity with the Corallinaeae subfamily Corallinoideae. However, if it were a nongeniculate coral-
Figure 5. a-b: *Lithophyllum (Tenarea?) lithothamnioides* Maslov, 1962; a, contorted and branching laminar plants with bilateral growth of a single system of radiating filaments that grew and curved outwards to both sides; note the preserved epithallial cells at the tip of some filaments (arrows); b, detail showing the frequently fused cells of adjacent filaments (arrow). c, *Lithophyllum pavlovii* Maslov, 1956; longitudinal section of the fan-like arranged filaments with laterally well-aligned primary cell walls; note the cell fusions between adjacent filaments (arrows). d-f: *Lithophyllum platticarpum* Maslov, 1962; d, detail of the ventral core; e, sections of lenticular to moustache-shaped, small, uniporate conceptacles; f, detail of a uniporate conceptacle with a relatively large and conical pore canal (p); note the frequent cells fusions between adjacent filaments (arrows).
Lithophyllum platticarpum Maslov, 1962
Figs. 5d-f

1962 Lithophyllum platticarpum Maslov, 88-89, pl. 26, figs. 1-3, text-fig. 66.
1973 Lithophyllum platticarpum Maslov; Maslov, pl. 18, fig. 10.
? 1977 Leptolithophyllum platticarpum; Orszag-Sperber, Poignant & Poisson, 290, pl. 3, fig. 4.
? 1988 Leptolithophyllum platticarpum (Maslov) Poignant; Studenci, 45-46, pl. 15, fig. 3.
? 1989 Leptolithophyllum platticarpum (Maslov) Poignant; Piser & Studenci, 202, pl. 11, fig. 5.
? 1994 Lithophyllum platticarpum Maslov; Vannucci et al., pl. 1, fig. a.

Holotype: Designated by Maslov (1962, p. 88), thin section 383/8, illustrated in pl. 26, figs. 1-3 and text-fig. 66.

Age and locality: Badenian (Tortonian in Maslov, 1962), village Ljuben Velikij, west of Lvov, western Ukraine.

Examination of the type material: The only remaining thin section contains several fragments of plants similar to the ones illustrated by Maslov (1962: pl. 26, figs. 1-3 and text-fig. 66; Fig. 1) when he established L. platticarpum. Some of the fragments are abraded and overgrown by conspecific plants (or re-generating thalli) or by other coralline algae.

The specimens named L. platticarpum consist of encrusting and dorsiventral monomorous thalli. Cell filaments run parallel to the substrate for short distances, forming a plumose ventral core (with cells 10-14 x 15-30 μm) and then curve upwards to become perpendicular to the dorsal surface. In both the ventral core and the peripheral region, cells of adjacent filaments are strongly fused, irregular in shape and relatively large (10-15 μm in diameter and 10-20 μm in height).

Conceptacles are uniporate. Conceptacle chambers are small (210-230 μm in diameter and 35-50 μm in height) and lenticular to moustache-shaped in section. The pore canal is conical and large (15 μm) in relation to the conceptacle chamber. This kind of size and shape is typical of gametangial conceptacles in species belonging to the Corallinaceae (subfamilies Mastophoroideae and Lithophylloideae, Tab. 1).

Remarks: Although the occurrence of cell fusions in the thalli and the preserved conceptacles in the holotype suggest that they are gametangial plants of the subfamily Mastophoroideae within the family Corallinaceae (Tabs. 1, 2), the lack of sporangial conceptacles prevents the inclusion of L. platticarpum in a defined genus within this subfamily. The size and shape of the conceptacles were the main characters used by Maslov (1962) to distinguish L. platticarpum from coralline algae with similar vegetative characters. These features, however, cannot be compared with those of tetrasporangial plants used to delimit other species within the subfamily and, therefore, do not warrant confidently maintaining L. platticarpum as a separate species. Future studies may show that the specimens named L. platticarpum by Maslov (1962) correspond to gametangial plants of an extinct or extant mastophoroid species, characterised by features shown in sporangial and gametangial thalli, already described or as yet unnamed. The name L. platticarpum might be used in the latter case. The thalli illustrated by Orszag-Sperber et al. (1977), Studenci (1988), Piser & Studenci (1989) and Vanucci et al. (1994) correspond to gametangial plants of mastophoroid species. However, it cannot be confidently ascertained whether they are conspecific with the type of platticarpum due to the lack of diagnostic features used to delimit genera and species within the subfamily. Orszag-Sperber et al. (1977) transferred Lithophyllum platticarpum to the genus Leptolithophyllum Airoldi, 1930. Independently of the status of the latter genus the new combination was not validly published according to the ICBN (Art. 33.3).

Lithophyllum premoluccense var. creticicum
Maslov, 1956
Figs. 6a-b

1956 Lithophyllum premoluccense var. creticicum Maslov, 118-119, pl. 31, fig. 2; pl. 34, fig. 6, text-fig. 49.
1962 Lithophyllum premoluccense var. creticicum Maslov; Maslov, 90, text-fig. 68.

Holotype: Designated by Maslov (1956, p. 119), thin section 3504/5168, illustrated in pl. 31, fig. 2; pl. 34, fig. 6, and text-fig. 49.

Age and locality: Late Cretaceous, Iora river basin, Georgia.

Examination of the type material: One thin section numbered 5168 which contains the specimen described, illustrated and designated by Maslov (1956) as the holotype (Fig. 1).

The specimen is a small abraded fragment, 1 mm long and 0.55 mm wide, that may correspond to a branch of a nongeniculate plant or to an intergenicula segment of a geniculate coralline alga. The fragment consists of a single system of radiating and dividing cell filaments. Primary cell walls are laterally well aligned, generating a coaxial organisation of arched rows of cells with various lengths (ranging from 7 to 9 μm in diameter and from 50 to 80 μm in length). Cells in the centre of each row are longer than the ones in the periphery. Walls separating adjoining filaments are well-defined and continuous, suggesting that adjacent cells are only connected by secondary pits. The pattern of cell rows in the lower part of the fragment suggests aborted branching or abrasion leaving only the central part of a branched thallus. A poorly preserved protuberant structure on the surface of one side may correspond to the tangential section of a conceptacle, but no features indicating the nature of the possible conceptacle are recognisable.

Remarks: The absence of cell fusions in the type of L. premoluccense var. creticicum indicates that it corresponds to a member of the subfamily Lithophylloideae
Figure 6. **a-b:** *Lithophyllum premoluccense* var. *cretacicum* Maslov, 1956; a, small abraded fragment consisting in a single system of radiating and dividing cell filaments with coaxial arrangement; the protuberant structure on the top surface (arrow) possibly corresponds to a tangential section of a conceptacle; b, detail of arched rows of laterally well aligned cells in the coaxial structure. **c-d:** *Lithophyllum senonicum* Maslov, 1956; c, section of the only specimen, an abraded fragment with a core of coaxial cell filaments which curve outwards to become perpendicular to the thallus surface; d, detail of figure 6c showing cell fusions (arrows) and the change in cell size from the core to the periphery; **e-f:** *Lithophyllum translucidum* Maslov, 1956; e, small fragment of a monomorous plant showing the radiating and dividing cell filaments which curve outwards to become almost perpendicular to the outer surface of the thallus; f, detail of filaments with cell fusions (arrow) and the tangential section of the conceptacle.
in the family Corallinaceae. The lack of other significant features, however, prevents any confident assignment of *L. premoluccense* var. *cretacicum* to known genera within this subfamily (Tabs. 1, 2).

*Lithophyllum senonicum* Maslov, 1956

Figs. 6c-d

1956 *Lithophyllum senonicum* Maslov, 118, pl. 34, fig. 3, text-fig. 48.

1962 *Lithophyllum senonicum* Maslov; Maslov, 92, text-fig. 10.

**Holotype:** Designated by Maslov (1956, p. 118), thin section 3504/5127, illustrated in pl. 34, fig. 3, text-fig. 48.

**Age and locality:** Maastrichtian, Iora river basin, Georgia.

**Examination of the type material:** One thin section numbered 5127, which contains the specimen described and illustrated by Maslov (1956) (Fig. 1). The specimen consists of an oblique section of a small, abraded fragment of a coralline fruticose branch 2 mm long and 1 mm wide. It may be a branch of a nongeniculate coralline alga or an intergenicula segment of a geniculate plant. The thallus shows monomerous construction with a single system of cell filaments that are coaxially arranged in rows in the core and curve outwards to become perpendicular to the thallus surface. The cells both in the core and in the peripheral region are connected by cell fusions. Cell size changes from row to row, but is always longer in the core (8-10 μm in diameter and 35-50 μm in height) than in the periphery of the thallus (7-9 μm in diameter and 20-25 μm in length). No conceptacles are present.

**Remarks:** The occurrence of cell fusions excludes the assignment of *L. senonicum* to the subfamily Lithophylloideae, but the lack of other significant characters prevents its inclusion in any defined generic or suprageneric taxon within the Hapalidiaceae, or the Corallinaceae subfamily Mastophoroideae or subfamily Corallinoideae (Tabs. 1, 2).

*Lithophyllum translucidum* Maslov, 1956

Figs. 6e-f

1956 *Lithophyllum translucidum* Maslov, 121-122, pl. 36, fig. 2, text-fig. 53.

1962 *Lithophyllum translucidum* Maslov; Maslov, 92-93, text-fig. 61-62.

**Holotype:** Designated by Maslov (1956, p. 122), thin section 3504/5038, illustrated in pl. 36, fig. 2, text-fig. 53.

**Age and locality:** Late Senonian, Kahetia region, Georgia.

**Examination of the type material:** The only remaining thin section contains the specimen illustrated by Maslov (1956) (Fig. 1). It is a small fragment (1.1 mm long and 0.53 mm thick) of a plant with monomerous construction consisting of a system of radiating and dividing cell filaments, which curve outwards to become almost perpendicular to the outer surface of the thallus. This fragment may be the remains of a branch of a nongeniculate plant or of an intergenicula segment of a geniculate coralline alga. Primary cell walls in adjacent filaments are relatively well-aligned and coaxially arranged. Cells are 9-10 μm in diameter and 40-44 μm in length. The cells of adjoining filaments are connected by cell fusions. The section tangentially cuts a conceptacle chamber on one side of the thallus, but it is unclear whether it is uni- or multiporate.

**Remarks:** The presence of cell fusions excludes the assignment of *L. translucidum* to the subfamily Lithophylloideae, but the lack of other significant characters prevents its inclusion in any defined generic or suprageneric taxon within the Hapalidiaceae, or the Corallinaceae subfamily Mastophoroideae or subfamily Corallinoideae (Tab. 1).

**TAXA INVOLVING MISSING TYPES**

The holotypes designated by Maslov (1956) of the following two species names were not found in the Maslov collection of in the Geological Institute of the Russian Academy of Sciences of Moscow. There are, however, thin sections containing coralline algae attributed to these species and illustrated in later works by Maslov (1962, 1973).

*Melobesia (Lithoporella) parasitica* Maslov, 1956

Fig. 7

1956 *Melobesia (Lithoporella) parasitica* Maslov; 161-162, pl. 64, text-fig. 82.

**Figure 7.** *Melobesia (Lithoporella) parasitica* Maslov, 1956; section of several superimposed, small, unistratose, encrusting plants.
1962 *Melobesia (Lithoparella) parasitica* Maslov; Maslov, 100, pl. 23, figs. 1-3; pl. 27; text-fig. 79.
1973 *Melobesia (Lithoparella) parasitica* Masl.; Maslov, pl. 18, fig. 5.

**Holotype:** Designated by Maslov (1956, p.162), thin section 350/1448, illustrated in pl. 64, and text-fig. 82.

**Age and locality:** Badenian (Tortonian in Maslov, 1956), western slope of Vysokaja Tura, Toltry mountains, village Gumenzy, Opol’e, Ukraine.

**Examination of the collection:** The only remaining thin section in the Maslov collection is the one numbered 387, which is not the holotype (Fig. 1); instead, it contains plants later illustrated by Maslov (1962, pl. 23, fig. 1). There are several superimposed, small unistratose, dimerous plants. Their cells (10-13 μm in diameter and 16-18 μm in length) seem to be joined by cell fusions. No reproductive structures are recognisable.

**Remarks:** The lack of significant vegetative features, together with the absence of any reproductive structures, prevents any assignment of the specimens attributed by Maslov (1962) to *Melobesia (Lithoparella) parasitica* to known generic taxa within the Corallinales (Tab. 2). The occurrence of cell fusions would suggest an affinity with the Corallinaceae subfamily Mastrophoroideae or the Hapalidiaceae subfamily Melobesioideae. The actual nature of the “problematic conceptacle” drawn by Maslov (1956, text fig. 82a) in the protologue of the species remains uncertain since the holotype thin section was not found.

*Lithophyllum (Dermatolithon) ucrainicum*
Maslov, 1956

**Holotype:** Designated by Maslov (1956, p. 159), thin section 350/60, illustrated in pl. 62, figs. 1-3 and text-fig. 80.

**Age and locality:** Badenian (Tortonian in Maslov, 1956), Toltry mountains, village Gumenzy, Opol’e, western Ukraine.

** Examination of Maslov’s material:** There are two thin sections on which the name *L. (D.) ucrainicum* is written: 350 and another not numbered. The latter is also labelled as “paratype” in the handwriting of a curator of Maslov’s collection. None of them, however, is the one designated as the holotype by Maslov (1956). The plants in sample 350 were illustrated by Maslov (1962) in pl. 24, figs.1 and 2. The remaining thin sections contain several plants and superimposed applanate branches of one to several plants with vegetative characters similar to those illustrated among coralline plants that belong to other taxa. They are all dorsiventral and dimerous with a ventral layer of primigenous filaments of squarish to palisade cells. Short postigenous filaments, comprising up to 5 cells, may arise perpendicularly from the ventral layer. Well-defined cell walls separating adjacent filaments indicate the absence of cell fusions. Sections of uniporate conceptacles can be observed in plants in the two thin sections. They are prominent on the thallus surface and hemispherical in shape. Conceptacle floors are situated 1 to 3 cell layers deep in the surrounding vegetative portion of the thallus.

**Remarks:** The vegetative and reproductive features of the plants included by Maslov (1962) in *L. (D.) ucrainicum* indicate that they can be assigned to *Lithophyllum*, in particular they reveal a strong resemblance to fossil and living plants of *L. pustulatum* (Lamouroux) Foslie. However, the lack of the holotype thin section and the uncertain features shown by the plants illustrated by Maslov (1956) when he established this name make it difficult to ascertain whether the plants in the remaining thin sections are conspecific with the ones in the designated type. While the specimen in pl. 62, fig. 3 (Maslov, 1956) might be a portion of a thallus similar to the plants described by the author in 1962, the vegetative characters of the plants in pl. 62, figs. 1 and 2 (Maslov, 1956) are obscure and difficult to interpret. In the absence of the designated holotype sample the circumscription of *L. (D.) ucrainicum* will remain doubtful.

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**REFERENCES**


Bassi, D., Zakrevskaya, E. & Fugagnoli, A. 2002. A guide to the collections of Vladimir Maslov (Rhodophyta, Cora-


Bory, J.B. 1832. Notice sur les polypiers de la Grèce. Expédition Scientifique Morée (Section Sciences Physiques), 3, 204-209.


Penrose, D. & Woelkerling, W.J. 1992. A reappraisal of
**Hydrolithon** (Corallinaeae, Rhodophyta) and its relationships to *Spongites*. *Phycologia*, **21**, 81-88.


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