



Re-assessment of the type collections of Maslov's species of Hapalidiales (Rhodophyta). Species originally attributed to *Lithothamnium*, *Mesophyllum* and *Palaeothamnium*

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ABSTRACT

This is the third and last paper of a series devoted to the revision of the types of the species and infra-specific taxa of coralline red algae established in two monographs by Maslov (1956a, 1962). Maslov was a Russian palaeontologist who described many taxa of fossil calcareous algae from the former USSR from 1929 to 1973. As in other publications from those decades, Maslov's new species and infraspecific taxa were separated by characters of questionable significance from a modern taxonomic point of view. In this study, as in previous contributions, a number of types of fossil coralline algae in Maslov's original collection are re-assessed with a modern morpho-anatomic taxonomic approach. The collection consists of thin sections currently housed in the Geological Institute of the Russian Academy of Sciences of Moscow. This paper deals in particular with the types of species attributed by Maslov to the genera *Lithothamnium*

RESUMEN

Este es el tercer y último artículo de una serie dedicada a la revisión de los tipos de especies y taxones infra-específicos de algas coralinas establecidos por Maslov (1956a, 1962) en dos monografías. Maslov fue un paleontólogo ruso que describió muchos taxones de algas calcáreas fósiles de la antigua Unión Soviética entre 1929 y 1973. Como en otras publicaciones de esa época, Maslov separó las nuevas especies y taxones infra-específicos con caracteres diagnósticos cuestionables desde la perspectiva de la taxonomía moderna de las algas coralinas. En este trabajo, como en los dos anteriores, se revisan tipos de la colección original de Maslov, que consiste en láminas delgadas depositadas en el Instituto Geológico de la Academia de Ciencias de Rusia en Moscú. En particular, este artículo trata de las especies atribuidas por Maslov (1956a, 1962) a los géneros *Lithothamnium* (= *Lithothamnium*), *Mesophyllum* y *Palaeothamnium* (Hapalidiales, Rhodophyta). Sólo el

(as *Lithothamnium*), *Mesophyllum* and *Palaeothamnium* (Hapalidiales, Rhodophyta). According to our reassessment, only the type of *Mesophyllum schenckii* var. *corticesum* (as *Mesophyllum schenckii* var. *corticesum*) can be confidently assigned to a currently accepted genus within the family Hapalidiaceae, subfamily Melobesioideae. The types of *Lithothamnion iorii*, *Palaeothamnium kossovense*, *Mesophyllum kutense*, *Lithothamnion microcellulosum*, *Lithothamnion prae-fructiculosum*, and *Lithothamnion tchernomoricum* possess multiporate conceptacles and non-coaxial ventral core and can be attributed to the subfamily Melobesioideae. The lack of epithallial cells, however, prevents any precise generic assignment within the *Lithothamnion*, *Phymatolithon*, *Clathromorphum* and *Synarthrophyton* complex. Finally, the lack of significant characters prevents any confident attribution of the type of '*Lithothamnion saxorum* var. *korolukae*' to any defined generic or suprageneric taxon within the Hapalidiales or the Corallinales. The absence of reproductive structures in the types of '*Lithothamnion caucasicum*', '*Lithothamnion (?) intergeminum*', and '*Lithothamnion (?) suhumii*' prevents the placement of these taxa in any order and family within Hapalidiales, Corallinales or Sporolithales.

Keywords: Calcareous algae, taxonomy, Melobesioideae, Hapalidiales, Rhodophyta.

tipo de *Mesophyllum schenckii* var. *corticesum* (como *Mesophyllum schenckii* var. *corticesum*) puede ser asignado con certidumbre a un género actualmente aceptado dentro de la familia Hapalidiaceae, subfamilia Melobesioideae. Los tipos de *Lithothamnion iorii*, *Palaeothamnium kossovense*, *Mesophyllum kutense*, *Lithothamnion microcellulosum*, *Lithothamnion prae-fructiculosum* y *Lithothamnion tchernomoricum* presentan conceptáculos multiporados y región ventral no coaxial y pueden ser incluidos dentro de la subfamilia Melobesioideae. No obstante, la ausencia de células epiteliales impide una adscripción genérica precisa dentro del complejo *Lithothamnion*, *Phymatolithon*, *Clathromorphum* y *Synarthrophyton*. La imposibilidad de observar la naturaleza de los conceptáculos impide una asignación precisa del tipo de '*Lithothamnion saxorum* var. *korolukae*' a una familia o subfamilia dentro de Hapalidiales o Corallinales. Finalmente, la ausencia de caracteres relevantes impide atribuir los tipos de '*Lithothamnion caucasicum*', '*Lithothamnion (?) intergeminum*', y '*Lithothamnion (?) suhumii*' a ningún taxón genérico o supragenérico dentro de las Hapalidiales, Corallinales o Sporolithales.

Palabras clave: Algas calcáreas, taxonomía, Melobesioideae, Hapalidiales, Rhodophyta.

1. INTRODUCTION

Vladimir Petrovich Maslov was a Russian author who worked from 1929 to 1973 on Silurian to Miocene sedimentary rocks from the former USSR (Bassi *et al.*, 2002). His research concentrated on benthic calcareous algae and he published a number of contributions on the palaeontology and biostratigraphic significance of fossils of this group. His main results were presented in two monographs published by the Russian Academy of Sciences of Moscow in 1956 and 1962. In these monographs, he described a large number of coralline algal species and infra-specific taxa (67 in 1956 and 97 in 1962), establishing 41 new taxa (Bassi *et al.*, 2002). As in other palaeontological studies of the 20th century, the diagnostic criteria used by Maslov (1956a, 1962) to separate genera and infra-generic taxa are different from those used in the present-day morpho-anatomic taxonomy of coralline algae. Therefore, the significance of the taxon names in a modern taxonomic context cannot be fully assessed from the original illustrations and descriptions in Russian by Maslov (1956a, 1962). The large number of taxa established by Maslov warranted the interest of re-studying his original collections in order to identify the types of the taxa, select lectotypes for taxa with no previously established type, and describe and illustrate the types

focusing on characters with diagnostic relevance. This paper is the fifth contribution to the taxonomic revision of taxa described by Maslov. Previous contributions focused on the study of the encrusting foraminifer *Solenomeris afonensis* Maslov, originally described as an alga (Bassi, 2003), the re-assessment of the coralline genera established by Maslov (Bassi *et al.*, 2005), the re-examination of the types of the species attributed by Maslov (1956a, 1962) to *Lithophyllum* and *Melobesia* (Braga *et al.*, 2005), and to *Archaeolithothamnium* (Bassi *et al.*, 2007).

2. MATERIAL AND METHODS

The original material of Maslov is preserved as thin sections stored mostly in two boxes at the laboratory of palaeophycology in the Geological Institute at the Russian Academy of Sciences of Moscow. No hand samples from which the thin sections were cut are conserved. The study of thin-sections was performed using light microscopy. The terminology for anatomical descriptions follows Woelkerling (1988) and Braga *et al.* (1993), cell and conceptacle dimensions follow Chamberlain *et al.* (1988) and coralline-algal growth-forms are described according to Woelkerling *et al.* (1993).

In accordance with ICN Article 61 (particularly 61.4; McNeill *et al.*, 2012), the orthography of names has been standardized, and errors corrected. Non-standardized variants and other incorrect spellings used by authors are given in parentheses (i.e., *Mesophyllum schenckii* var. *corticesum* as *Mesophyllum schenckii* var. *corticesum*; *Lithothamnium* as *Lithothamnium*).

3. SYSTEMATIC PALAEOLOGY

Order HAPALIDIALES Nelson, Sutherland, Farr et Yoon, 2015

Family **Hapalidiaceae** Gray, 1864

Subfamily Melobesioideae Bizzozzero, 1885

Genus *Mesophyllum* Lemoine, 1928

The genus *Mesophyllum* was established by Lemoine (1928) for coralline algae possessing a coaxial core (hypothallium) and multiporate asexual conceptacles. This has also been the traditional palaeontological concept of the genus (Lemoine, 1939; Conti, 1943; Mastrorilli, 1973; Braga *et al.*, 1993; Aguirre & Braga, 1998; Basso *et al.*, 1998; Braga, 2003; Iryu *et al.*, 2009, 2012; Aguirre *et al.*, 2011, 2012). Woelkerling & Harvey (1993), however, suggested that spermatangial initials forming simple spermatangial

filaments and development of male conceptacle roof from filaments surrounding the spermatangial initials were the only diagnostic characters separating *Mesophyllum* from other melobesioid genera with relatively similar vegetative characters, namely *Clathromorphum* and *Synarthrophyton*. As spermatangia are not calcified, their preservation potential as fossils is very low, and they are rarely preserved. Consequently, the traditional concept of *Mesophyllum* continues to be used. In a similar way, Peña *et al.* (2011) only used vegetative characters to include a new living melobesioid species in *Mesophyllum* (*Mesophyllum sphaericum*). As they were unable to observe spermatangial conceptacles, these authors considered the presence of a strongly coaxial medulla composed of concentric arching tiers a character separating *Mesophyllum* from *Synarthrophyton*, in which coaxial areas are usually more localized. According to Peña *et al.* (2011) the occurrence of more than one epithallial cell in peripheral filaments in *Clathromorphum* (Adey, 1970; Adey & Johansen, 1972; Lebednik, 1977; Woelkerling, 1988; Harvey *et al.*, 1994; Basso *et al.*, 2004) separates this genus from *Mesophyllum*.

Two of the eleven species and infraspecific taxa re-assessed here were originally ascribed to *Mesophyllum* by Maslov (Table 1). Basically, Maslov followed Lemoine (1928) and included in *Mesophyllum* all non-geniculate coralline red algae that have multiporate tetrasporangial conceptacles and a coaxial ventral core (Maslov, 1956a: 13; 1962: 23). Only one, however, shows features warranting its inclusion in *Mesophyllum*.

Table 1. Taxonomic disposition of the eleven Maslov's species re-assessed in the present study. Classification system in the left column is that used by Maslov and in common use during the period of Maslov's studies. In that scheme, all corallines were placed in a single family (the Corallinaceae) and all species lacking genicula were referred to a single subfamily (the Melobesiae). Classification system in the right column used in the present study follows Harvey *et al.* (2003a, b), Braga (2003), and Nelson *et al.* (2015).

Maslov's disposition	Disposition proposed in this paper
Family Corallinaceae	Order HAPALIDIALES Nelson, Sutherland, Farr et Yoon, 2015
Subfamily Melobesiae	Family HAPALIDIACEAE Gray, 1864
	Subfamily Melobesioideae Bizzozzero, 1885
	<i>Mesophyllum</i> Lemoine, 1928
<i>Mesophyllum Schenckii</i> var. <i>corticesum</i> Maslov, 1956	<i>Mesophyllum schenckii</i> var. <i>corticesum</i>
<i>Lithothamnium</i> (?) <i>iorii</i> Maslov, 1956	uncertain generic placement
<i>Palaeothamnium kossovense</i> Maslov, 1962	uncertain generic placement
<i>Mesophyllum kutense</i> Maslov, 1962	uncertain generic placement
<i>Lithothamnium microcellulosum</i> Maslov, 1956	uncertain generic placement
<i>Lithothamnium prae-fruticulosum</i> Maslov, 1956	uncertain generic placement
<i>Lithothamnium tchernomoricum</i> Maslov, 1956	uncertain generic placement
	Order and family uncertain
<i>Lithothamnium saxorum</i> var. <i>Korolukae</i> Maslov, 1956	uncertain generic placement
<i>Lithothamnium caucasicum</i> Maslov, 1956	uncertain generic placement
<i>Lithothamnium</i> (?) <i>intergeminum</i> Maslov, 1962	uncertain generic placement
<i>Lithothamnium</i> (?) <i>suhumii</i> Maslov, 1956	uncertain generic placement

Mesophyllum schenckii var. *corticesum* Maslov, 1956a
(Figs 1a, 2a-2b)

1956a *Mesophyllum schenckii* var. *corticesum* var. nov.
Maslov; Maslov, p. 163-164, Pls. 65-67, Text-fig. 84 (as
Mesophyllum schenckii var. *corticesum*)

1962 *Mesophyllum schenckii* var. *corticesum* Maslov;
Maslov, p. 76, Pl. 15, Text-fig. 54 (as *Mesophyllum*
schenckii var. *corticesum*)

Lectotypification. In describing *Mesophyllum schenckii* var. *corticesum*, Maslov (1956a: 163-164) cited a single thin section numbered 1048 and designated it as holotype. After examining that thin section, however, we have concluded that Maslov based his account on material belonging to two different taxa, thus necessitating designation of a lectotype (ICN Art 9.2, 9.14).

One taxon, designated here as lectotype of *Mesophyllum schenckii* var. *corticesum* and illustrated here in Figs 2a-2b and identifiable in Maslov (1956a: pl. 65, fig. 2), is characterized by an encrusting to foliose growth-form, a conspicuously coaxial core, and comparatively small multiporate conceptacles. The other taxon, not illustrated here but visible along with the lectotype in Maslov (1956a: pl. 65, fig. 2), consists of part of a protuberance with numerous comparatively large buried multiporate conceptacles and a basal region with a plumose ventral core. In accord with ICN Art 9.14, the encrusting to foliose, coaxial material has been designated as lectotype because corresponds more nearly with the original description (Maslov 1956a: 163-164). The protuberant thallus has not been identified, but the lack of a coaxial core excludes it from *Mesophyllum*.

Remaining individuals illustrated in the protologue (Maslov 1956a: pl. 65, fig. 1; pl. 66, figs 1-2; pl. 67, figs 1-2; text-fig. 84) do not occur in thin-section 1048, and we have not found them on other thin-sections examined during this study.

Age and locality. Badenian (Middle Miocene), Opolie, road Lagodov-Sivorosch, western slope of Vysokaja Tura, Lvov province, West Ukraine.

Examination of the lectotype of *Mesophyllum schenckii* var. *corticesum*. The designated lectotype includes encrusting-foliose undulating thalli or branches of a single thallus, up to 500 μm in thickness. The thalli have a dorsiventral organization and monomerous construction with a single system of filaments that are coaxially arranged in the ventral core (ca. 100-200 μm thick) and curve to become perpendicular to the thallus surface. Cells in the coaxial core are about 10-15 μm in diameter and 30-35 μm long. The peripheral region is 200-250 μm thick and shows zonation. Cell length decreases from bottom to top in several growth zones (75-120 μm

thick), and are about 8-10 μm in diameter and 12-15 μm high in the dorsal portion. Cell fusions are conspicuous. No epithallial cells are evident.

Two multiporate conceptacles are present (chambers: 225 μm in diameter and 175 μm high; 300 μm in diameter and 160 μm high; Figs 2a-2b). One of them is filled with adventitious cells. The pore canals are hardly visible and seem to be surrounded by cells similar to others in the conceptacle roof.

Remarks. The presence of cell fusions and multiporate conceptacles in the holotype means that *Mesophyllum schenckii* var. *corticesum* belongs to the Hapalidiaceae, subfamily Melobesioideae. These features combined with the coaxial growth of the core filaments result in placement in *Mesophyllum* as traditionally circumscribed. The status of *Mesophyllum schenckii* var. *corticesum* remains uncertain. The photographs and description of the holotype of *Mesophyllum schenckii* Howe, 1934 (Howe, 1934: 512-513, pl. 52, note the spelling of the name by Maslov, 1956a, 1962, is different) indicate that this species encompasses plants with protuberances. Examination of the isotype (Woelkerling, 1998) sent by the author to the Muséum d'Histoire Naturelle, Paris (Howe, 1934, p. 511) confirms the occurrence of protuberances in Howe's species. In the original interpretation of *Mesophyllum schenckii* var. *corticesum* by Maslov (1956a), the taxon included plants with protuberances as well. As discussed before, the lectotype is restricted to encrusting-foliose plants and it is difficult to assess whether it can be considered conspecific with *M. schenckii*. The size and shape of conceptacles is similar in both taxa. The shape and size of cells surrounding the conceptacle pores are similar to cells in the rest of filaments in conceptacle roof in the examined isotype of *M. schenckii*. This character relevant in the separation of species of *Mesophyllum* (Harvey *et al.*, 2003a; Kaleb *et al.*, 2011) cannot be conclusively observed in the lectotype of *Mesophyllum schenckii* var. *corticesum*.

Mesophyllum schenckii var. *corticesum* has been identified by Fravega *et al.* (1984, 1993, no illustration) in the Miocene deposits of the Piedmont Basin (NW Italy).

3.1. Melobesioid taxa of uncertain generic placement

Remarks. Nine of the 12 species dealt with in this paper were originally ascribed to *Lithothamnion* by Maslov (1956a), who used the rejected name *Lithothamnium* Philippi, 1837 (Woelkerling, 1985; Table 1). Maslov (1956a: 14; 1962: 57) followed Lemoine (1911) and included in *Lithothamnion* non-geniculate coralline red algae with multiporate (tetrasporangial) conceptacles, monomerous construction, and non-coaxial core. *Phymatolithon* and *Clathromorphum*, which show these same features, were

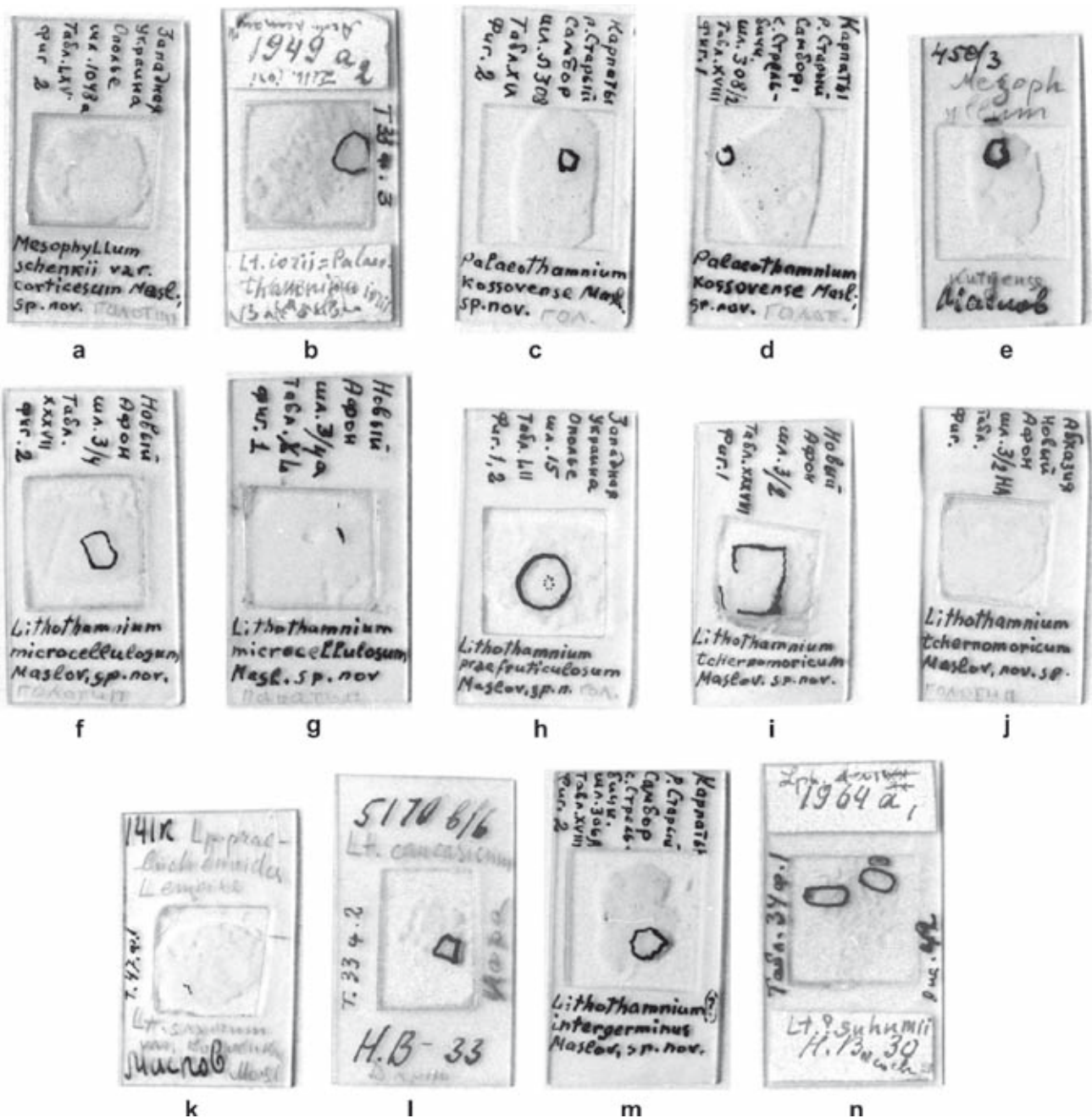


Figure 1. Thin sections from Maslov's collection at the Geological Institute, Russian Academy of Sciences, Moscow. **a)** *Mesophyllum schenckii* var. *corticesum* (as *Mesophyllum schenckii* var. *corticesum*) Maslov, 1956a; 1048, holotype. **b)** *Lithothamnium* (?) *iorii* Maslov, 1956a; 3504/1949a/2, holotype. **c, d)** *Palaeothamnium kossovense* Maslov, 1956a; 308, holotype; 308/2. **e)** *Mesophyllum kutense* Maslov, 1962; 450/3, holotype. **f, g)** *Lithothamnium microcellulosum* Maslov, 1956a; 3504/3/4, holotype; 3504/3/4a. **h)** *Lithothamnium praefruticulosum* Maslov, 1956a; 15, '*Lithothamnium praefruticulosum* Maslov sp. n.', holotype. **i, j)** *Lithothamnium tchernomoricum* Maslov, 1956a; 3504/3/2, holotype; 3504/3/2HA. **k)** *Lithothamnium saxorum* var. *korolukae* Maslov, 1956a; 3504/141. **l)** *Lithothamnium caucasicum* Maslov, 1956; 5170b. **m)** *Lithothamnium* (?) *intergeminum* Maslov, 1962; 306JI, holotype. **n)** *Lithothamnium* (?) *suhumii* Maslov, 1956a; thin section 1964a of the type collection.

rejected as distinct genera by Lemoine (1911). In his first monograph, Maslov (1956a: 14) who did not mention *Clathromorphum*, indicates that *Phymatolithon* is characterised by concave conceptacle roofs but the genus is not cited again in his later publications.

Nine genera of Melobesioideae are recognized in modern accounts of living coralline algae (Harvey *et al.*, 2003a, b) and five of them include species with monomeric construction that do not show coaxial growth. According to the modern concept of the genus, *Lithothamnium* includes

only those Melobesioideae with monomerous construction throughout, in which the distal walls of epithallial cells are flattened and flared (Woelkerling, 1983, 1985, 1988; Harvey *et al.*, 2003a). This latter character separates *Lithothamnion* from the other monomerous melobesioid genera: *Clathromorphum*, *Kvaleya*, *Mesophyllum*, *Phymatolithon*, and *Synarthrophyton*. A strongly coaxial core can be used to distinguish *Mesophyllum* from the rest of the members of the subfamily (see above; e.g., Peña *et al.*, 2011) and *Kvaleya* is a monospecific genus based on a small, “parasitic” species which shows haustoria penetrating the host cells. *Phymatolithon* might also be separated from other monomerous melobesioids as it presents subepithallial initials as short as or shorter than the immediately subtending cells while initials in the rest of the genera are as long as or longer than the underlying cells. Uncalcified or developmental features, such as spermatangial filaments or male conceptacle development, can also be used to separate genera within the subfamily Melobesioideae but they are very rarely preserved in fossil thalli. If only calcified features are taken into account, *Lithothamnion* cannot be separated from *Phymatolithon*, *Clathromorphum* and *Synarthrophyton* in the absence of epithallial cells, which also prevents the identification of subepithallial initials. Epithallial cells are frequently preserved in fossil coralline thalli and can be used to recognize *Lithothamnion* (Braga *et al.*, 1993; Aguirre *et al.*, 1996, 2012; Vannucci *et al.*, 2010) or *Phymatolithon* (Rasser & Piller, 1999). In most fossil monomerous melobesioids with non-coaxial core, however, epithallial cells are not preserved or their poor preservation does not allow to confidently assessing whether they are flared. In all these cases, the application of modern botanical taxonomy implies that the specimens cannot be assigned to any defined genus and must be considered as indeterminate Melobesioideae (e.g., Iryu *et al.*, 2009, 2012). The correct application of the current taxonomy for living corallines to fossil thalli, therefore, involves the impossibility of using a large number of species names established in the palaeontological literature based upon species types lacking epithallial cells. Some of these species names, however, were established on types showing other

remarkable characters, which might potentially be used to identify and name fossil melobesioids at the specific level, even if the species could not be assigned to any particular genus (e.g., Aguirre & Braga, 1998; Vannucci *et al.*, 2009, 2010; Aguirre *et al.*, 2011, 2012; Iryu *et al.*, 2012). This is the case of five of the Maslov’s species of hapalidiales originally attributed to *Lithothamnion* (as *Lithothamnium*) and *Palaeothamnium*.

Lithothamnion iorii Maslov, 1956a
(Figs 1b, 2c-2e)

1956a *Lithothamnium* (?) *iorii* sp. nov. Maslov, 1956a; Maslov, p. 115-116, Pl. 33, Fig. 3, Text-fig. 45

1962 *Palaeothamnium iorii* Maslov; Maslov, p. 53-54, Text-fig. 28

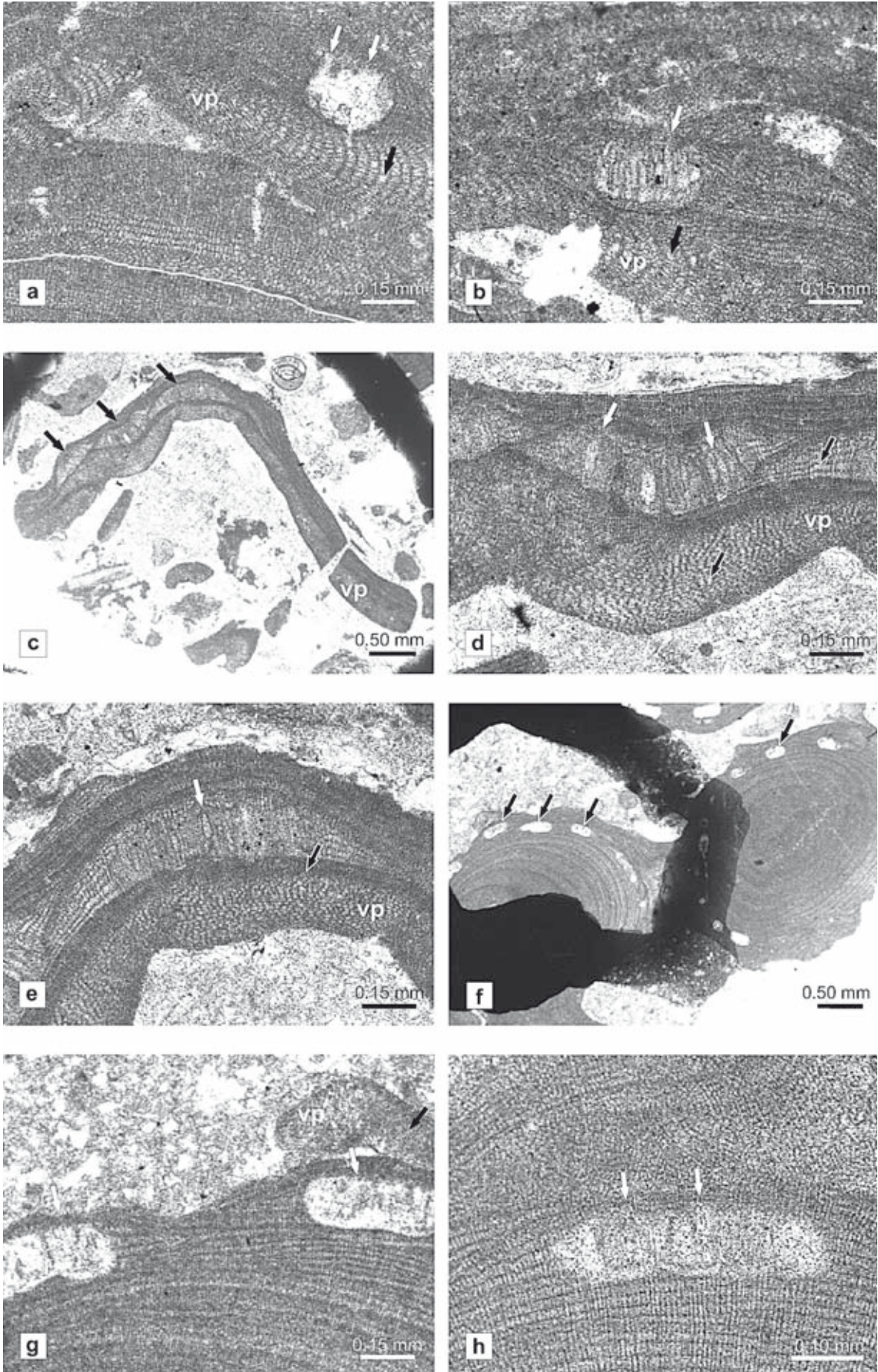
Basionym. *Lithothamnion* (?) *iorii* Maslov (as *Lithothamnium*), 1956a, p. 115-116, Pl. 33, Fig. 3, Text-fig. 45.

Holotype. Designated by Maslov (1956a: 116), thin section 3504/1949a/2, labelled ‘Lt iorii = Palaeothamnium iorii Maslov’, illustrated in pl. 33, fig. 3, text-fig. 45 (Fig. 1b).

Age and locality. Danian, Iori river, Caucasus, Georgia.

Examination of the holotype. The thin section containing the holotype includes one thin encrusting undulating thallus, 625 µm thick and up to 6.3 mm long (Fig. 2c). The thallus has a dorsiventral monomerous organization with a plumose ventral core 190-250 µm thick (Figs 2d-2e). The section is oblique to the filaments but it shows that they curve dorsally to become perpendicular to the thallus dorsal surface. The peripheral region ranges from 250 µm to 300 µm in thickness. Cells are about 8-10 µm in diameter and 20-30 µm long in the core region. In the peripheral region, the cells decrease in length from bottom to top of marked growth zones parallel to the thallus surface (8-10 µm in diameter and 10-15 µm high) and are particularly larger at the flanks of developing conceptacles (about 10-15 µm in diameter and up to 20

Figure 2. a-b) *Mesophyllum schenckii* var. *corticesum* Maslov, 1956a, lectotype, thin section 1048, labelled ‘Mesophyllum schenckii var. *corticesum* Masl. sp. nov.’; **(a, b)** longitudinal and oblique sections of an encrusting-foliose thallus showing the coaxial arrangement of the ventral filaments (vp) with cell fusions (black arrows) between adjacent cell walls and multiporate conceptacles (white arrows point to pore canals). **c-e)** *Lithothamnion iorii* Maslov, 1956a, holotype, thin section 3504/1949a/2, labelled ‘Lt iorii = Palaeothamnium iorii Maslov’; **(c)** thin encrusting undulating thallus bearing three multiporate conceptacles (arrows); **(d-e)** close-ups of multiporate conceptacles showing the thick plumose ventral core (vp), cell fusions (black arrows) and the elongated cells perpendicular to the surface of the conceptacle roof (white arrows). **f-h)** *Lithothamnion kutense* (Maslov), holotype, thin section 450/3, labelled as ‘Mesophyllum kutense Maslov’; **(f)** oblique transversal sections of two branches showing conceptacles (arrows) localized in the outer growth stage of the thallus; **(g)** close-up of Fig. 2f showing the renewed growth with a plumose ventral core (vp, black arrow) and multiporate conceptacles (white arrows); **(h)** detail of a multiporate conceptacles showing the pore canals (arrows).



μm high). Cells of adjacent filaments are connected by cell fusions. No epithallial cells and subepithallial initials can be recognized.

Oblique sections of three young or immature conceptacles are present. They protruded above the surrounding thallus surface and are 500-600 μm in diameter and 200-250 μm high (protologue data: 300-500 μm in diameter and 100 μm high). Remnants of filaments involved in conceptacle formation, with elongated cells perpendicular to the roof surface, which are characteristic of multiporate conceptacles, can be observed within the conceptacles (Figs 2d-2e) but not fully developed pore canals occur.

Remarks. The occurrence of cell fusions and multiporate conceptacles in the holotype supports placement of this taxon in the Hapalidiaceae, subfamily Melobesioideae (e.g., Harvey *et al.*, 2003a, b). Maslov (1962) attributed this species to the genus *Palaeothamnium* Conti 1946, characterised by the elongation of cells during tetra/bisporangial conceptacle development according to its author (Basso *et al.*, 1997). Aguirre *et al.* (1996), however, demonstrated that such elongation occurs in several genera of the subfamily Melobesioideae and considered *Palaeothamnium* a younger heterotypic synonym of *Lithothamnium*. The absence of epithallial cells in the type of *Lithothamnium iorii* Maslov, 1956a prevents any confident generic assignment of the species within the subfamily Melobesioideae.

This species has been reported in the Paleocene and Early Eocene of Corsica, Paris Basin, Aude (France), Sardinia and SE Calcareous Alps (Poignant & Chaffaut, 1970; Poignant, 1977; Dieni *et al.*, 1979; Segonzac, 1979; Moussavian, 1993) and Early Oligocene from the NW India (Misra *et al.*, 2001). Its status as a distinct species and its relationships to other melobesioids is uncertain.

Palaeothamnium kossovense Maslov, 1962
(Figs 1c-1d, 3)

1962 *Palaeothamnium kossovense* Maslov; Maslov, p. 54-56, Pl. 18, Figs 1, 4, Pl. 19, Figs 1-4, Text figs 29-32

1988 *Palaeothamnium kossovense* Maslov; Studencki, p. 19, Pl. 3, Figs 2, 5

1989 *Palaeothamnium kossovense* Maslov; Pisera & Studencki, p. 195, Pl. 6, Fig. 1

Basionym. *Palaeothamnium kossovense* Maslov, 1962, p. 54-56, Pl. 18, Figs 1, 4, Pl. 19, Figs 1-4, Text-figs 29-32.

Age and locality. Paleocene, Staryj Sambor (village Strel'bichi), Karpathians, Ukraine.

Holotype. Maslov (1962: 54) designated as holotype the thin section 308, labelled 'Palaeothamnium kossovense

Masl. sp. nov., 308' (Fig. 1c). In the protologue, immediately below the name, the author refers to tab. 19, figs 1-4 and text-figs 29-32 as illustrations of the species. However, only the picture in tab. 19, fig. 2 corresponds to the thallus in section 308. The rest of thalli illustrated in tab. 19, figs 1, 3 and 4, as well as in tab. 18, figs 1-2 and 4 (not mentioned in the text) do not appear either in section 308 or in section 308/2, conserved in the collection and also labelled 'Palaeothamnium kossovense Masl. sp. nov.' (Fig. 1d). They probably were in the lost thin sections mentioned in the protologue (223/26, 249, and 306/2, that might be an erratum for 308/2).

Examination of the holotype. The holotype (thin section 308) is an abraded thallus fragment 4.5 mm long and 2.75 mm wide, probably part of a protuberance of a larger thallus (Fig. 3a). The thallus has a dorsiventral monomerous organization with a thick ventral plumose core (up to 0.37 mm thick) in which the filaments run parallel to the ventral surface for a very short distance and curve upwards while dividing to become perpendicular to the dorsal surface (Fig. 3c). Core region cells are mostly 8-12 μm in diameter and 20-25 μm long (protologue data: 5-7 μm in diameter and 10-25 μm long). Cells in the peripheral region slightly decrease in size from bottom to top of faintly defined growth zones and are 5-8 μm in diameter and 10-20 μm high (protologue data: 5-7 μm in diameter and 10-20 μm high). Cell fusions are present. There is a clear lateral alignment of cells of adjacent filaments. No epithallial cells or subepithallial initials are preserved.

Three structures consisting of elongated cells overlying a layer of cells larger than the ones in the rest of the peripheral region can be interpreted as remains of immature conceptacles that have become buried in the thallus (Figs 3d-3f). Elongation of cells in the conceptacle primordium is a common feature of development of tetra/bisporangial conceptacles in melobesioids (see Aguirre *et al.*, 1996 for references). Elongated and larger "cells", wider than surrounding filaments probably correspond to developing tetra/bisporocytes. The structures are 160-180 μm wide and 70-100 μm in height. No pore canals can be observed at the top of the structures.

Remarks. The occurrence of cell fusions and developing multiporate conceptacles in the holotype indicate that it belongs to the Hapalidiaceae, subfamily Melobesioideae. The inclusion of this species in *Palaeothamnium* Conti 1946 by Maslov (1962) was based on the occurrence of structures with elongated cells in the specimens that he examined and described. This feature, however, reflects the initial steps of conceptacle development in melobesioids and cannot be considered diagnostic at the genus level (Aguirre *et al.*, 1996). Although the type species of *Paleothamnium* (*P. archaeotypum*) belongs to

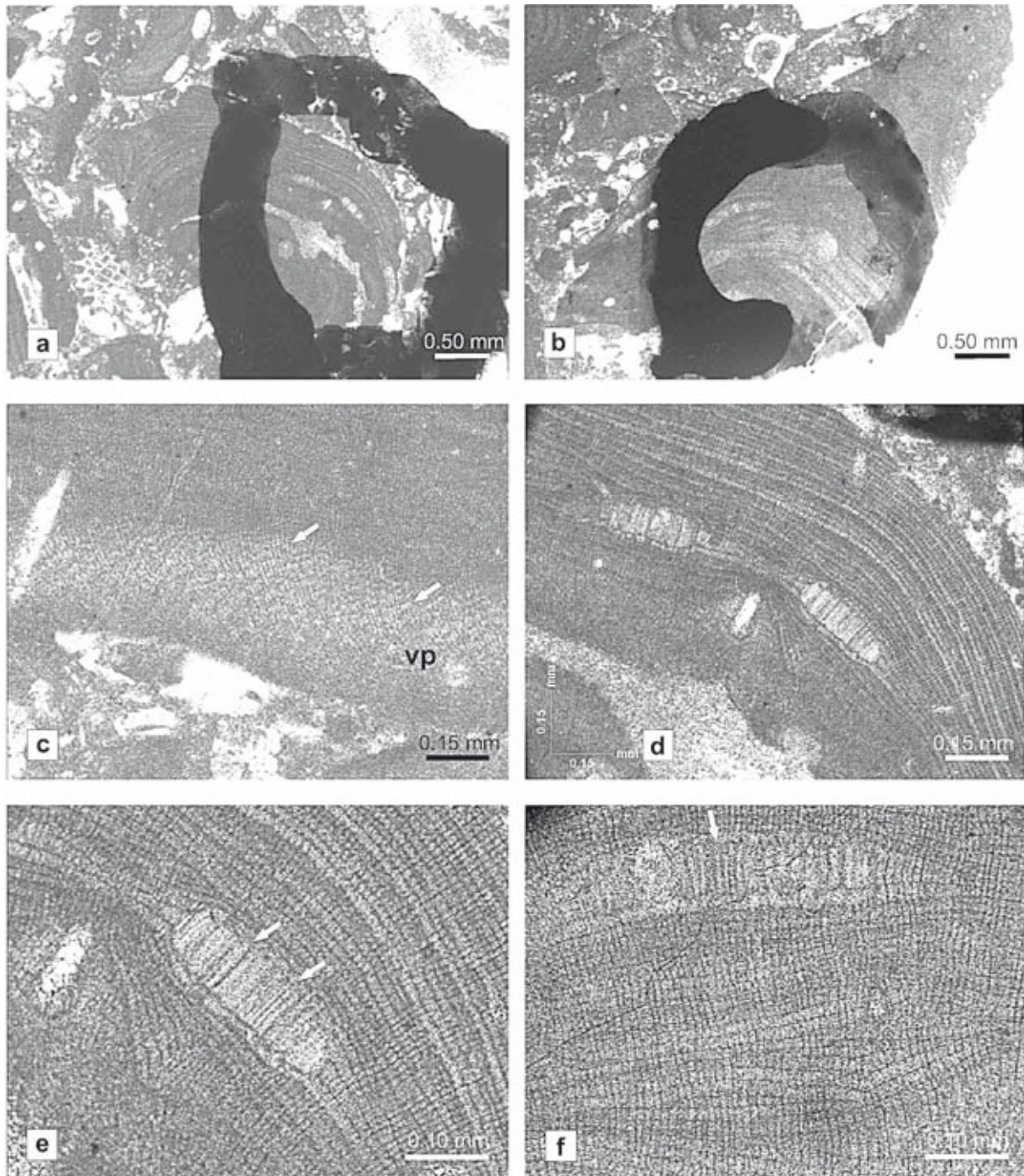


Figure 3. *Palaeothamnium kossovense* (Maslov); **a, c-e**) holotype (thin section 308); **b, f**) (thin section 308/2). **a-b**) Nearly longitudinal sections of protuberances. **c**) Part of the thick ventral plumose core (vp) in which cell fusions are present (arrows). **d-f**) Close-ups of the structures (**d-e** are from **a**; **f** is from **b**), characterized by elongated cells (arrows) possibly representing immature conceptacles that have become buried in the thallus.

Lithothamnion (Aguirre *et al.*, 1996), *Palaeothamnium kossovense* Maslov, 1962 cannot be confidently assigned to any genus within the subfamily Melobesioideae due to the lack of epithallial cells in its type.

This species has been reported in the Paleocene and Early Eocene from the Carpathian Mountains, Sardinia and

SE Calcareous Alps (Poignant & Caffautt, 1970; Dieni *et al.*, 1979; Moussavian, 1993) and Middle Miocene from Poland (Studencki, 1988; Pisera & Studencki, 1989).

Mesophyllum kutense Maslov, 1962
(Figs 1e, 2f-2h)

1962 *Mesophyllum kutense* sp. nov. Maslov; Maslov, p. 75-76, Pl. 17, Fig. 2, Text-fig. 53

Holotype. Designated by Maslov (1962: 76), thin section 450/3, labelled as 'Mesophyllum kutense Maslov' (Fig. 1e). Text-fig. 53 is a drawing of an oblique tangential section of the multiporate conceptacle illustrated in pl. 17, fig. 2.

Age and locality. Paleogene, Stari Kut, West Ukraine.

Examination of the holotype. The holotype shows an oblique transversal section of two branches joined by a bridge of an encrusting part of the thallus (Fig. 2f). The sections of the large branches are 2.5 mm x 2.0 mm and 2.5 mm x 3.0 mm, respectively. The thallus is monomerous with a plumose ventral core observable in renewed growth, about 80 µm thick, over previous thallus surfaces marked by conceptacle roofs (Fig. 2g). Cells in the core are about 6 µm in diameter and 12 µm long (no protologue data). Length of cells in the peripheral region decrease in size from bottom to top of faint growth zones (5-8 µm in diameter and 10-15 µm high; protologue data: 6 µm in diameter by 8-16 µm high). Cells of adjacent filaments are connected by cell fusions. No epithallial or subepithallial cells can be recognised.

There are eight multiporate conceptacles present. In their longitudinal-tangential sections they are relatively flat with round sides and slightly protruded on the thallus surface (chambers 300-350 µm in diameter and 100-170 µm high; protologue data: 140-360 µm in diameter by 80-140 µm high). The pore canals are cylindrical (10-15 µm in diameter and 30-40 µm high; Fig. 2h).

Remarks. The presence of cell fusions and multiporate conceptacles in the holotype places *Mesophyllum kutense* within the family Hapalidiaceae, subfamily Melobesioideae (e.g., Braga, 2003; Table 1). The absence of coaxial growth precludes placement of the type in *Mesophyllum* as traditionally delimited by palaeontologists (see above) and the absence of epithallial cells prevents its placement in any of the other monomerous non-coaxial melobesioideid genera. Consequently, *Mesophyllum kutense* Maslov,

1962 is treated here as other monomerous non-coaxial fossil melobesioideids lacking preserved epithallial cells. Its status as a distinct species and its relationships to other melobesioideids are uncertain.

This species name has had a low impact in the palaeophycological literature since it has been referred only three times in Early Miocene deposits from Italy (Fravega *et al.*, 1993, no illustration).

Lithothamnium microcellulosum Maslov, 1956a
(Figs 1f-1g, 4a-4c)

1956a *Lithothamnium microcellulosum* sp. nov. Maslov; Maslov, p. 136, Pl. 37, Fig. 2, Pl. 40, Fig. 1.

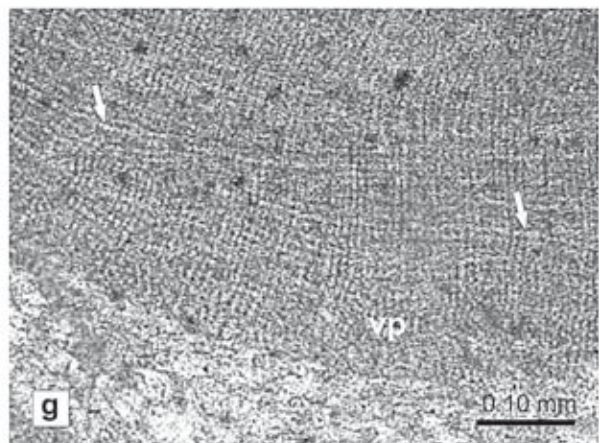
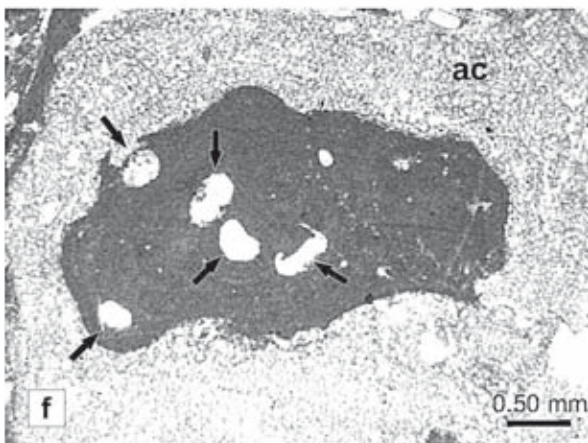
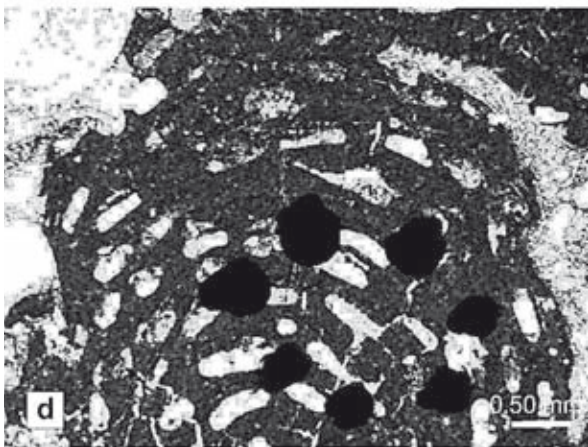
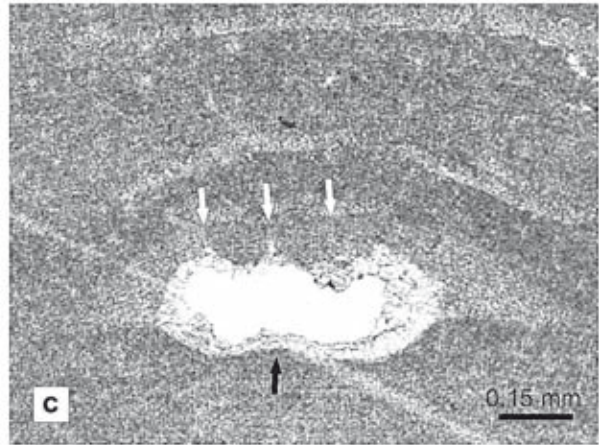
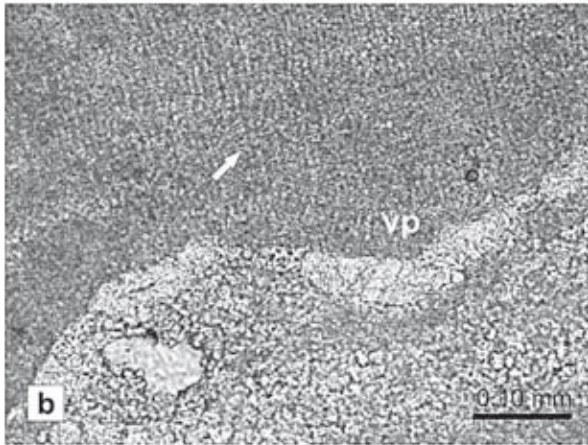
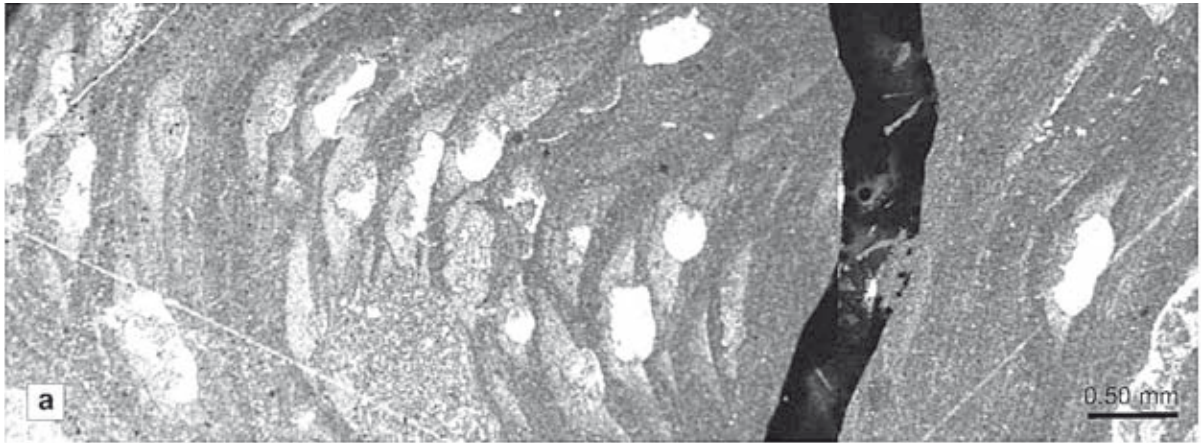
1962 *Lithothamnium microcellulosum* Maslov; Maslov, p. 65-66, Text-fig. 40.

Holotype. Designated by Maslov (1956a: 136), thin section 3504/3/4 (Fig. 1f). This section contains the specimen illustrated in pl. 37, fig. 2. There is another thin section from the same sample, labelled 3504/3/4a (Fig. 1g), which according to the handwriting on its surface should include the detail illustrated in pl. 40, fig. 1. However, we were not able to identify the part of the thallus shown in that picture. The same conceptacle in the holotype shown in pl. 37, fig. 2 was also illustrated as a drawing in text-fig. 40 in Maslov (1962).

Age and locality. Early Eocene, limestones with "Nummulites"; Novyj Afon, Abkhazia, Georgia.

Examination of the holotype. The holotype only contains an abraded fragment 6.5 mm long and 4 mm wide, of a protuberance. The section shows superimposed thalli or successive growth stages of a single thallus with dorsiventral monomerous organization with a non-coaxial ventral core of filaments (Fig. 4b). The filaments in the core run parallel to the ventral surface only for a very short distance and immediately bend upwards. Cells in the ventral core are 5-8 µm in diameter and 10-15 µm long and cells in the peripheral region are 5-10 µm in diameter and 10-15 µm high (protologue data: 4-7 µm in diameter and 7-10 µm high). Cells of adjacent filaments are connected

Figure 4. a-c) *Lithothamnium microcellulosum* Maslov, 1956a, holotype, thin section 3504/3/4. **(a)** Longitudinal oblique section of a protuberance showing superimposed thalli bearing multiporate conceptacles; **(b)** close-up of Fig. 4a showing the non-coaxial ventral core of filaments (vp) with cell fusions (arrow); **(c)** multiporate conceptacle protruding above surrounding thallus surface with an undulated floor higher at its centre (black arrow) and round sides. **d-e)** *Lithothamnium prae-fruticulosum* Maslov, 1956a, thin section 3504/15, labelled as 15, 'Lithothamnium prae-fruticulosum Maslov sp. n.'; **(d)** longitudinal section of the lumpy protuberance showing several growth stages with multiporate conceptacles; **(e)** close-up of Fig. 4d illustrating a longitudinal oblique section of a multiporate flat conceptacle with rounded sides (arrows point to pore canals). **f-g)** *Lithothamnium tchernomoricum* Maslov, 1956a, holotype, thin section 3504/3/2; **(f)** the abraded fragment of a thallus protuberance, encrusted by an acervulinid foraminifer (ac), with buried conceptacles (arrows); **(g)** the transversal section of the ventral part (vp) of the thallus does not show the thallus organization (arrows point to cell fusions).



by cell fusions. No distinct growth zones occur but growth stages are marked by renewed growth over the surface of buried conceptacles. No distinct epithallial or subepithallial cells can be recognized.

There are eight multiporate conceptacles present (chambers 500-600 μm in diameter and 225-250 μm high; protologue data: 500 μm in diameter and 100-150 μm high; Figs 4a, 4c). The conceptacles protrude above surrounding thallus surface. The larger sections of conceptacles show an undulated floor higher at its centre and round sides. In these sections, the base of conceptacle roof is undulated as well. The floor seems to "carve" the underlying peripheral filaments. Cells at the conceptacle flanks and roof are larger and less calcified than surrounding cells in the peripheral region. Conceptacle roofs are 10-15 (16) cell thick. Pore canals are *c.* 35 μm in diameter and 70-75 μm high. Cells lining the pore canals are poorly preserved.

Remarks. The type of *Lithothamnium microcellulosum* Maslov, 1956a, with multiporate conceptacles and cell fusions, belongs to the Hapalidiaceae, subfamily Melobesioideae but cannot be confidently attributed to any genus within this subfamily due to the lack of epithallial cells in its type. Its status as a distinct species and its relationships to other melobesioids is uncertain.

This species has been reported in the Eocene of the Republic of Macedonia (Lemoine, 1977), Oligocene-Early Miocene of Italy (Mastrorilli, 1973), and Middle Miocene of Poland (Studencki, 1988).

Lithothamnium praefruticulosum Maslov, 1956a
(Figs 1h, 4d-4e)

1956a *Lithothamnium praefruticulosum* sp. nov.
Maslov; Maslov, p. 149-150, Pl. 52, Figs 1-2.

1962 *Lithothamnium praefruticulosum* Maslov; Maslov,
p. 68, Pl. 16, Figs 1, 3.

1968 *Lithothamnium praefruticulosum* Maslov;
Mastrorilli, p. 266-267, Pl. 8, Fig. 3.

1983 *Lithothamnium praefruticulosum* Maslov;
Bosence, p. 153-156, Text-fig. 4, Pl. 16, Figs 1-2.

1985 *Lithothamnium praefruticulosum* Maslov;
Pisera, p. 101, Pl. 20, Figs 1-3.

1989 *Lithothamnium praefruticulosum* Maslov; Pisera
& Studencki, p. 196-197, Pl. 7, Fig. 4, Pl. 8, Fig. 5.

Holotype. Designated by Maslov (1956a: 150), thin section 3504/15, now labelled as 15, 'Lithothamnium praefruticulosum Maslov sp. n.', with reference to the type locality and figures in the protologue (Fig. 1h). A portion of the thin section is marked by an ink circle.

Age and locality. Badenian (Middle Miocene), Opolie, Lvov province, West Ukraine.

Examination of the holotype. The holotype consists of a longitudinal oblique section of an abraded fragment of a lumpy protuberance 4.5 mm long and 4 mm wide, with several growth stages marked by buried conceptacles (Fig. 4d). The ventral side of the thallus cannot be observed but in renewed growth of the thallus over conceptacle roofs the organisation is monomerous with a very thin plumose ventral core of filaments that curve upwards after running parallel to the ventral surface for a very short distance. In the peripheral part of the thallus, cells are 20-22 μm in diameter and 20-22 μm long (protologue data: 15 μm in diameter and 15-20 μm long). Cells of adjacent filaments are connected by cell fusions. No epithallial cells or subepithallial initials can be recognized.

Longitudinal-tangential sections of more than 20 multiporate conceptacles are present. They are relatively flat (chambers 400-500 μm in diameter and 130-150 μm high; protologue data: 250-350 μm in diameter by 180-200 μm high) with rounded sides and slightly protruded on the thallus surface. The roof is 4-6 cell thick and the pore canals are cylindrical (20-25 μm in diameter and 50-70 μm high; Fig. 4e).

Remarks. The presence of cell fusions and multiporate conceptacles indicate that the holotype of *Lithothamnium praefruticulosum* Maslov, 1956a belongs to the Hapalidiaceae, subfamily Melobesioideae but the species cannot be assigned to a genus within the family due to the absence of preserved epithallial cells in the holotype. Its status as a distinct species is uncertain.

This species has been reported in the Oligocene-Late Miocene of the Piedmont Basin (Mastrorilli, 1968, 1973; Fravega & Vannucci, 1982; Fravega *et al.*, 1984, 1993), Early Miocene of Corsica (Bellini & Mastrorilli, 1975), Middle Miocene of Poland (Studencki, 1988; Pisera & Studencki, 1989), Middle Miocene of the Transilvanian Basin in Romania (Bucur & Filipescu, 1994), Late Miocene of Malta (Bosence, 1983).

Lithothamnium tchernomoricum Maslov, 1956a
(Figs 1i-1j, 4f-4g, 5a)

1956a *Lithothamnium tchernomoricum* sp. nov. Maslov;
Maslov, p. 136-137, Pl. 38, Figs 1-5, Pl. 39, Figs 1-2

1962 *Lithothamnium tchernomoricum* Maslov; Maslov,
p. 71, Pl. 17, Text-fig. 49

Holotype. Designated by Maslov (1956a: 137), thin section 3504/3/2 (Fig. 1i). This is the thin section containing the thallus illustrated in the protologue in pl. 38, fig. 1 and pl. 39, figs 1-2. The thallus fragments illustrated in pl. 38, fig. 2, together with *Solenomeris* have not been identified neither in this section nor in the additional one from the same hand sample (3504/3/2/HA) also preserved in the collection. We have not been able to identify the

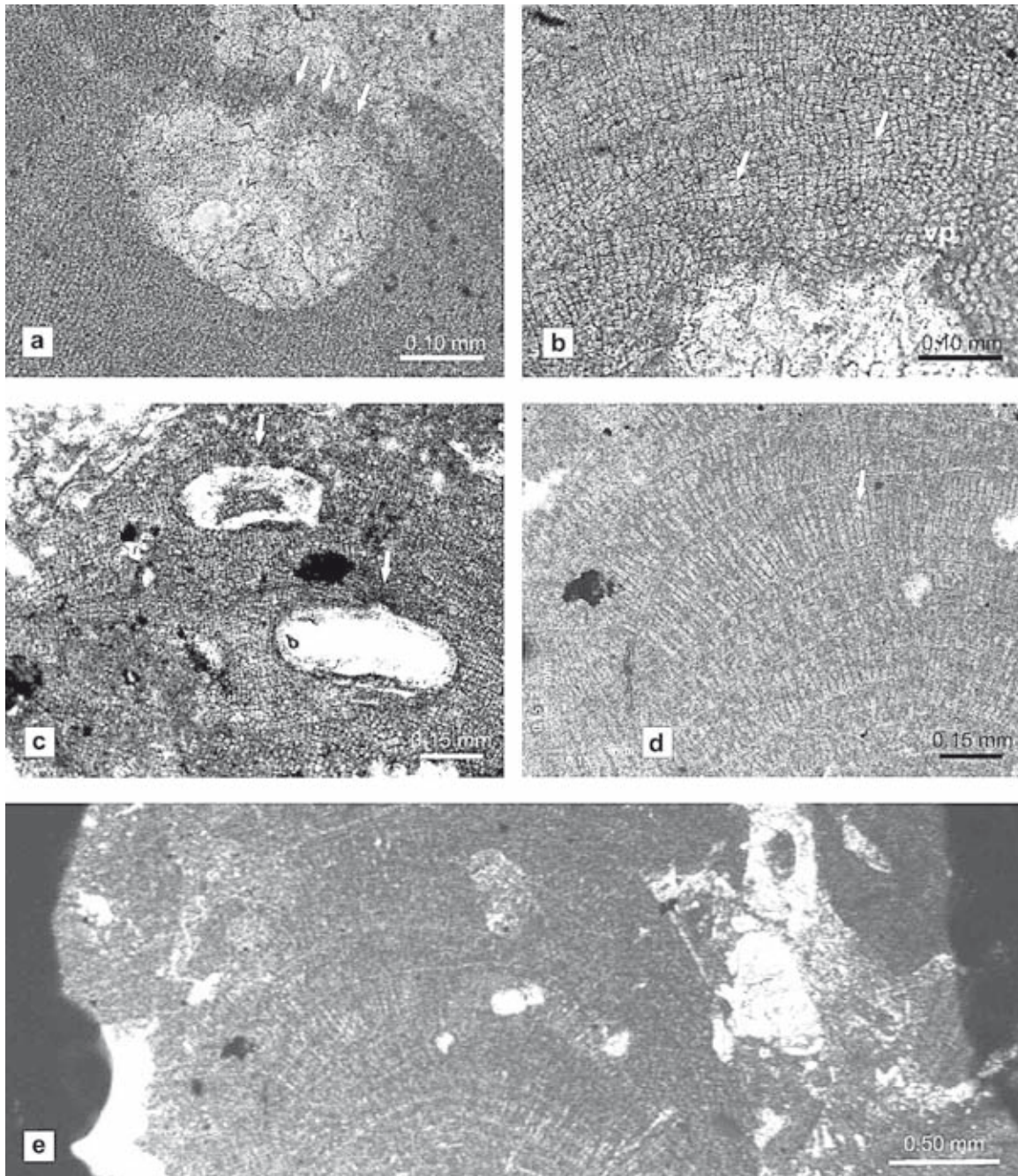


Figure 5. **a)** *Lithothamnion tchernomoricum* Maslov, 1956a, holotype; oblique section of a multiporate conceptacle showing cylindrical pore canals (arrows). **b-c)** *Lithothamnium saxorum* var. *korolukae* Maslov, 1956a, thin section 3504/141, 'Lt saxorum var. Korolukae Masl, Lp praelichenoides Lemoine, pl. 47'; **(b)** plumose core of filaments (vp) showing cell fusions between cells of adjacent filaments (arrows); **(c)** oblique longitudinal sections of two possible uniporate (arrows) conceptacles. **d-e)** *Lithothamnion intergeminum* Maslov, 1962, holotype, thin section 306JI, labelled as 'Lithothamnium (?) intergeminum Maslov sp. nov.'; **(d)** detail of Fig. 5e showing the fan-like arrangement of the filaments in the protuberance (arrow, cell fusions); **(e)** oblique section of the protuberance.

cell groups illustrated in drawings in pl. 38, figs 3-5. These three drawings were again published by Maslov in 1962 (text-fig. 49).

Age and locality. Early Eocene, limestones with "Nummulites"; Novyj Afon, Abkhazia, Georgia.

Examination of the holotype. The holotype consists of a longitudinal oblique section of an abraded fragment of a thallus protuberance, 3.5 mm long and 2.0 mm wide, with several growth stages marked by buried conceptacles. This fragment constitutes the nucleus of a small macroid made up of an encrusting acervulinid foraminifer (Fig. 4f).

The section does not allow to assess the nature of the thallus organization and the type of ventral core. Cells in the protuberance are about 10 µm in diameter and 20 µm long (protologue data: 7 µm in diameter by 7 µm long) with faint growth zones. Cells of adjacent filaments are connected by cell fusions (Fig. 4g). No epithallial cells or subepithallial initials are preserved.

Oblique sections of five multiporate conceptacles buried in the thallus are present (350-500 µm in diameter and 220-250 µm high; protologue data: 220-250 µm in diameter by 100 µm high). One shows cylindrical pore canals about 25 µm in diameter and 40 µm high (Fig. 5a).

Remarks. The presence of cell fusions and multiporate conceptacles in the holotype means that *Lithothamnion tchernomoricum* Maslov, 1956a belongs to the Hapalidiaceae, subfamily Melobesioideae (Table 1). The thallus depicted in Figure 4g is sectioned transversally the direction of core filament growth and, as consequence, the ventral core is not evident because one is seeing a cross section of it rather than a section parallel to the core filaments. As neither the type of thallus organization nor the shape of epithallial cells can be observed in the type, no further precision in the taxonomic assignment can be made and we keep the basionym to refer to this species. This species has never been reported by authors other than Maslov (1956a, 1962, 1973).

3.2. Taxa of uncertain order and family placement

The types of the following four taxa, listed here by their basionym, do not show sufficient features to allow order and family placement within the Hapalidiales, Corallinales or Sporolithales (Table 1).

Lithothamnion saxorum var. *korolukae* Maslov, 1956a
(Figs 1k, 5b-5c)

1956a *Lithothamnium saxorum* var. *Korolukae* var. nov.
Maslov; Maslov, p. 144, Pl. 47, Text-fig. 65.

1962 *Lithothamnium saxorum* var. *korolukae* Maslov;
Maslov, p. 69, Text-fig. 46.

Holotype. Designated by Maslov (1956a: 144), thin section 3504/141, 'Lt saxorum var. Korolukae Masl, Lp praelichenoides Lemoine, pl. 47', (Fig. 1k). Text-fig. 65 is a drawing of a monomerous thallus organization that cannot be identified in the thallial fragment in this thin section.

Age and locality. Badenian (Middle Miocene), Toltry, West Ukraine.

Examination of the holotype. The holotype is an abraded fragment of an encrusting thallus, 1.65 mm long and up to 0.9 mm thick, intergrown with encrusting foraminifera. The thallus shows a dorsiventral monomerous organization with a plumose core of filaments that run parallel to the ventral surface for a short distance and curve upwards to become perpendicular to the thallus surface in the dorsal peripheral region (Fig. 5b). Core cells are 10-15 µm in diameter and 20-25 µm long (protologue data: 15 µm in diameter by 25-30 µm long); peripheral region cells are: 10-15 µm in diameter and 12-15 µm long (protologue data: 10-15 µm in diameter and 10-20 µm long). Cells of adjacent filaments are connected by cell fusions. No epithallial cells are preserved.

Oblique longitudinal sections of two possibly uniporate conceptacles are present (chambers 375-450 µm in diameter; 150-170 µm high; Fig. 5c). The sections, however, do not show conclusively whether the conceptacles are multiporate, as interpreted by Maslov (1962: 69) or uniporate.

Remarks. As the nature of the conceptacles in the holotype cannot be assessed *L. saxorum* var. *korolukae* cannot be attributed to any precise family and subfamily within Hapalidiales or Corallinales with non-geniculate thalli and cell fusions. This taxon has never been reported by other authors.

Lithothamnion caucasicum Maslov, 1956a
(Figs 1l, 6)

1956a *Lithothamnium caucasicum* sp. nov. Maslov;
Maslov, p. 116-117, Pl. 33, Fig. 2, Text-fig. 46.

1962 *Lithothamnium caucasicum* Maslov; Maslov, p.
60-61, Text-fig. 36.

Holotype. Designated by Maslov (1956a: 117), thin section 5170b, labelled 'Lt caucasicum, pl. 33, fig. 2' (Fig. 1l). Text-fig. 46 is a drawing of filaments that cannot be identified in the thallial fragment in this thin section.

Age and locality. Danian, Iori River, Caucasus, Georgia.

Examination of the holotype. The thin section includes two small abraded fragments, 3.5 mm long and 1.75 mm wide, and 3 mm long and 2.5 mm wide respectively, that probably correspond to transversal (left specimen in Fig. 6) and longitudinal (right specimen) sections of branches of non-geniculate thalli. The fragments consist of a single system of radiating and dividing filaments. Primary cell walls are not laterally aligned, ranging from 8 to 10 µm in diameter and from 20 to 25 µm in length. Cells in the centre of each branch are longer than the ones in the periphery. Walls separating adjoining filaments are

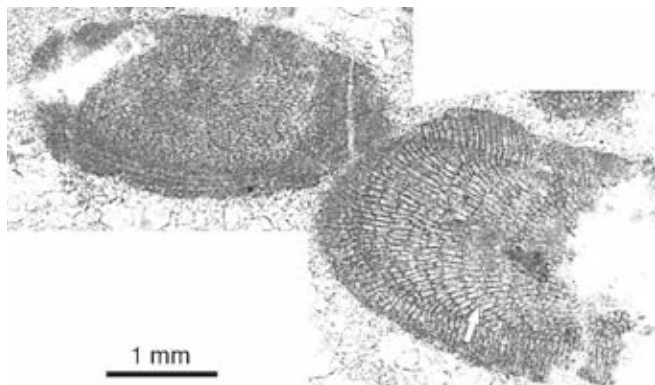


Figure 6. *Lithothamnium caucasicum* Maslov, 1956a, thin section 5170b, labelled 'Lt caucasicum, pl. 33, fig. 2'. Two small abraded fragments, constituting the holotype, with no reproductive structures preserved.

relatively well-defined but scarce cell fusions can be recognised. No reproductive structure is present.

Remarks. The occurrence of cell fusions indicates that the type of *Lithothamnium caucasicum* does not belong to the subfamily Lithophylloideae in the family Corallinaceae. However, the lack of other significant features, such as reproductive structures, prevents any confident assignment of *L. caucasicum* to known taxa within the Hapalidiales, Corallinales or Sporolithales (Table 1).

The name *L. caucasicum* has been used for algae from the Late Cretaceous of the Pyrenees (Poignant, 1981) and Paleocene deposits from Borneo (Johnson, 1966).

Lithothamnium (?) *intergeminum* Maslov, 1962
(Figs 1m, 5d-5e)

1962 *Lithothamnium* (?) *intergeminum* sp. nov. Maslov; Maslov, p. 62-63, Pl. 18, Fig. 2, Text-fig. 37.

Holotype. Designated by Maslov (1962: 62-63), thin section 306JI, labelled as 'Lithothamnium (?) intergeminus Maslov sp. nov.' (Fig. 1m). Text-fig. 37 is a drawing of five filaments that cannot be identified in the thallial fragment in this thin section. The holotype was illustrated in the protologue (Maslov, 1962, pl. 18, fig. 2). A portion of the thin section is marked by an ink circle.

Age and locality. Early Paleogene?, Staryi Sambor, Lvov province, West Ukraine.

Examination of the holotype collection. The thin section contains an oblique section of a protuberance (at least 2.5 mm in diameter) showing filaments with a fan-like arrangement (Fig. 5e). Cells are slightly longer in the center of the protuberance than in its margins (15 µm in

diameter and 37 µm in height; protologue data: 10-25 µm in diameter and 35-50 µm high). Cell fusions are common (Fig. 5d). No reproductive structures are present and no epithallial cells can be identified.

Remarks. In the protologue Maslov (1962) did not describe conceptacles. He considered "*Lithothamnium* (?) *intergeminum*" as a possible transitional form from "Solenopores" to the genus *Lithothamnium* (Maslov, 1956a: 63). The absence of reproductive structures precludes any certain placement at order or family levels within the Hapalidiales, Corallinales or Sporolithales (Table 1). This species has been only referred by Maslov (1962).

Lithothamnium (?) *suhumii* Maslov, 1956a
(Figs 1n, 7)

1956a *Lithothamnium* (?) *suhumii* sp. nov. Maslov; Maslov, p. 114, Text-fig. 42.

1962 *Lithothamnium* (?) *suhumii* Maslov; Maslov, p. 70, Text-fig. 47.

Basionym. *Lithothamnium* (?) *suhumii* Maslov (as *Lithothamnium*), 1956a, p. 114, Text-fig. 42.

Holotype. Designated by Maslov (1956a: 114), thin section 1964a 'Lt ? suhumii, 30, pl. 34, fig. 1' (Fig. 1n). Text-fig. 42 shows two drawings of monomerous thallial organizations that cannot be identified in the thallial fragment in this thin section.

Age and locality. Danian, Iori River, Caucasus, Georgia.

Examination of the holotype. The holotype consists of a longitudinal to oblique section of an encrusting thallus fragment, ca. 1.5 mm long and 0.6 mm thick. The thallus has a monomerous construction with a thick ventral core that is probably coaxial about 150 µm in width and a peripheral region 450 µm in width where core filaments or their derivatives curve outwards towards the dorsal surface (Fig. 7). Cells in the ventral region are mostly 20 µm long and 10 µm in diameter. Cells in the peripheral region decrease from 15 to 20 µm in length within the conspicuous growth zones and are 8 µm in diameter. Cells of adjacent filaments are connected by cell fusions. No reproductive structures or epithallial cells are preserved.

Remarks. The absence of reproductive structures prevents the placement of the holotype in any order and family within the Hapalidiales, Corallinales or Sporolithales. This species has been only reported by Maslov (1956a, 1962).

Table 2. Status of coralline red algal species described by Maslov (1935, 1936, 1950, 1955, 1956a, 1956b, 1962). °, Bassi (2003); *, Bassi et al. (2005); **, Braga et al. (2005); ***, Bassi et al. (2007); §, this paper. Type material of species in group (e) has not been found. For details see the text.

Status	Species
(a) Species retained under original generic names	<i>Karpathia sphaerocellulosa</i> Maslov, 1962* <i>Lithophyllum duplex</i> Maslov, 1962** <i>Mesophyllum schenckii</i> var. <i>corticesum</i> Maslov, 1956a§ <i>Palaeophyllum elegans</i> Maslov, 1950* <i>Palaeophyllum caucasicum</i> Maslov, 1950* <i>Solenophyllum paleozoicum</i> Maslov, 1935*
(b) New combinations	<i>Hydrolithon corculumis</i> (Maslov) Braga et al., 2005** <i>Karpathia nataliae</i> (Maslov) Bassi et al., 2005* <i>Solenophyllum johnsonii</i> (Maslov) Bassi et al., 2005* <i>Sporolithon afonense</i> (Maslov) Bassi et al., 2007*** <i>Sporolithon ferganense</i> (Maslov) Bassi et al., 2007*** <i>Sporolithon irinae</i> (Maslov) Bassi et al., 2007*** <i>Sporolithon lvovicum</i> (Maslov) Bassi et al., 2007***
(c) Heterotypic synonyms	<i>Solenomeris afonensis</i> Maslov, 1956a° (synonym of <i>Solenomeris ogormani</i> Douvillé, 1924)
(d) Uncertain generic placement	<i>Melobesia (Lithoporella) badjii</i> Maslov, 1956a** <i>Lithothamnion caucasicum</i> (as <i>Lithothamnium</i>) Maslov, 1956a§ <i>Lithophyllum conocristatum</i> Maslov in Krivin & Maslov, 1962** <i>Lithophyllum dioscurens</i> Maslov, 1956a** <i>Lithothamnion</i> (?) <i>intergeminum</i> (as <i>Lithothamnium</i>) Maslov, 1962a§ <i>Lithothamnion</i> (?) <i>iorii</i> (as <i>Lithothamnium</i>) Maslov, 1956a§ <i>Melobesia (Lithoporella) karpatica</i> Maslov, 1962** <i>Palaeothamnium kossovense</i> Maslov, 1962§ <i>Bicorium kusbassense</i> Maslov, 1956b* <i>Mesophyllum kutense</i> Maslov, 1962§ <i>Lithophyllum (Tenarea?) lithothamnioides</i> Maslov, 1962** <i>Lithothamnion microcellulosum</i> (as <i>Lithothamnium</i>) Maslov, 1956a§ <i>Lithophyllum microsporium</i> Maslov, 1962** <i>Melobesia (Lithoporella) parasitica</i> Maslov, 1956a** <i>Lithophyllum pavlovii</i> Maslov, 1956a** <i>Lithophyllum platticarpum</i> Maslov, 1962** <i>Lithothamnion praefruticulosum</i> (as <i>Lithothamnium</i>) Maslov, 1956a§ <i>Lithophyllum premoluccense</i> var. <i>cretacicum</i> Maslov, 1956a** <i>Lithothamnion saxorum</i> var. <i>korolukae</i> (as <i>Lithothamnium</i>) Maslov, 1956a§ <i>Lithophyllum senonicum</i> Maslov, 1956a** <i>Lithothamnion</i> (?) <i>suhumii</i> (as <i>Lithothamnium</i>) Maslov, 1956a§ <i>Lithothamnion tchernomoricum</i> (as <i>Lithothamnium</i>) Maslov, 1956a§ <i>Lithophyllum translucidum</i> Maslov, 1956a**
(e) Type material not found	<i>Archaeolithothamnion rude</i> var. <i>asiaticum</i> Maslov (as <i>Archaeolithothamnium</i>), 1936*** <i>Lithophyllum pavlovii</i> var. <i>irregularis</i> Maslov, 1956a <i>Lithothamnion alasanii</i> (as <i>Lithothamnium</i>) Maslov, 1956a <i>Lithothamnion bullaense</i> (as <i>Lithothamnium</i>) Maslov, 1956a <i>Lithothamnion microcellulosum</i> var. <i>junior</i> (as <i>Lithothamnium</i>) Maslov, 1956a <i>Lithothamnion microphyllum</i> (as <i>Lithothamnium</i>) Maslov, 1956a <i>Lithothamnion pannosum</i> (as <i>Lithothamnium</i>) Maslov, 1956a <i>Lithothamnion taurinense</i> var. <i>reticulatum</i> (as <i>Lithothamnium</i>) Maslov, 1956a <i>Lithothamnion toltraense</i> (as <i>Lithothamnium</i>) Maslov, 1956a <i>Melobesia parasitica</i> var. <i>grandis</i> Maslov, 1956a <i>Melobesia tarhankutica</i> Maslov, 1962 <i>Mesophyllum contractum</i> Maslov, 1956a <i>Mesolithon lithothamnioides</i> Maslov, 1955* <i>Palaeophyllum tesalii</i> Maslov, 1950* <i>Solenopora concentrica</i> Maslov, 1956a <i>Solenopora filiformis</i> var. <i>estonica</i> Maslov, 1962 <i>Solenopora russiensis</i> Maslov, 1956a <i>Solenopora spongoides</i> var. <i>iuchvii</i> Maslov, 1956a

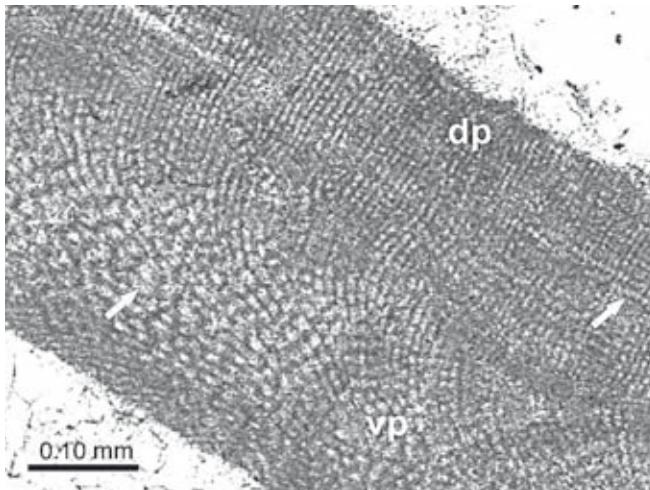


Figure 7. *Lithothamnion* (?) *suhumii* Maslov, 1956a, thin section 1964a 'Lt ? suhumii, 30, pl. 34, fig. 1'. Detail of the thick ventral core (vp) showing the possible coaxial arrangement of the filaments with cell fusions between adjacent cells (arrows). dp, dorsal portion.

4. CONCLUDING REMARKS

Eleven species originally ascribed to *Lithothamnion* (as *Lithothamnium*), *Mesophyllum* and *Palaeothamnium* by Maslov (1956a, 1962) are reassessed. Only the type of *Mesophyllum schenckii* var. *corticesum* Maslov, 1956a is assigned to the genus *Mesophyllum* Lemoine within the family Hapalidiaceae, subfamily Melobesioideae (Harvey *et al.*, 2003a, b). The types of *Lithothamnion iorii* Maslov, *Palaeothamnium kossovense* Maslov, *Mesophyllum kutense* Maslov, *Lithothamnion microcellulosum* Maslov, *Lithothamnion praefructiculosum* Maslov, and *Lithothamnion tchernomoricum* Maslov possess: a) multiporate conceptacles, b) cell fusions (diagnostic characters of the subfamily Melobesioideae), and c) non-coaxial ventral core. As no epithallial cells are preserved in the type material, they cannot be ascribed to a definite genus within *Lithothamnion-Phymatolithon-Clathromorphum-Synarthrophyton* complex. The lack of recognizable epithallial cells is common in fossil corallines making impossible to assign many fossil melobesioid species to one of the genera in this complex.

The type specimens of '*Lithothamnium saxorum* var. *korolukae* Maslov', '*Lithothamnion caucasicum* Maslov', '*Lithothamnion* (?) *intergeminum* Maslov', and '*Lithothamnion* (?) *suhumii* Maslov' do not contain sufficient diagnostic characters for placement in any genus or family within Hapalidiales, Corallinales or Sporolithales in a modern context, and we have retained the original names used by Maslov for recording purposes. Their status as distinct species is impossible to assess.

In the two Maslov's monographs (1956a, 1962) and in 1950, he described a large number of coralline algal species and infra-specific taxa (67 in 1956 and 97 in 1962), establishing 41 new taxa. After our taxonomic reassessments (Bassi, 2003; Bassi *et al.*, 2005, 2007; Braga *et al.*, 2005, and the present study), 6 species have been retained under original generic names, 7 species have been transferred to other genera, but their status as distinct species also requires further study, 2 species have been placed in the synonymy of other species, 23 species do not contain sufficient data to allow for placement in a genus in a modern context, and we have retained the original names used by Maslov for recording purposes (Table 2). We have been unable to locate the original material of 18 other non-geniculate coralline species described by Maslov.

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