REDESCRIPTION OF THE TYPE COLLECTIONS OF MASLOV'S SPECIES OF CORALLINALES (RHODOPHYTA). II. SPECIES INCLUDED BY MASLOV IN *Archaeolithothamnium* ROTHPLETZ, 1891

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ABSTRACT

Maslov described a large number of taxa of fossil calcareous algae, most belonging to Corallinales (Rhodophyta), in publications written in Russian and printed in the former USSR from 1929 to 1973. The type collections of these taxa are housed in the laboratory of palaeophycology in the Geological Institute at the Russian Academy of Sciences of Moscow. Maslov's species names must be taken into consideration in any taxonomic work dealing with corallinalean red algae, although their nomenclatural status and taxonomic significance need reassessment with a modern approach. Here we redescribe the types of four coralline algal species from lower Eocene and Miocene (Badenian) rocks of Abkhazia, Uzbekistan, and Ukraine attributed by Maslov (1956) to the genus *Archaeolithothamnium*. Our examination of *Archaeolithothamnium afonensis*, *A. ferganense*, *A. irinae*, and *A. keenanii* var. *lvovicum* leads us to transfer them to *Sporolithon*. The types are described and illustrated focusing on characters relevant in modern sporolithacean taxonomy. *Sporolithon irinae* (Maslov), comb. nov. is lectotypified.

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

RESUMEN

Maslov describió desde 1929 a 1973 numerosos taxones de algas calcáreas fósiles, la mayoría pertenecientes a las Corallinales (Rhodophyta), en publicaciones escritas en ruso y editadas en la antigua Unión Soviética. Las colecciones tipo que quedan de estos taxones se encuentran en el laboratorio de paleoficología del Instituto Geológico de la Academia Rusa de Ciencias de Moscú. Los nombres de especies de Maslov se deben tener en cuenta en cualquier trabajo sobre la taxonomía de algas rojas coralináceas, aunque su estatus nomenclatorial y su significado taxonómico tienen que ser revisados desde una perspectiva actualizada. En este trabajo estudiamos los tipos de cuatro especies de algas coralináceas del Eoceno inferior y del Mioceno (Badeniense) de Abjacia, Uzbekistan y Ucrania, incluídas por Maslov (1956) en el género *Archaeolithothamnium*. Transferimos *Archaeolithothamnium afonensis*, *A. ferganense*, *A. irinae*, y *A. keenanii* var.

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lvovicum a *Sporolithon*. Los tipos de estas especies son redescritos e ilustrados centrándonos en caracteres relevantes en la taxonomía moderna de la familia Sporolithaceae. Se designa el lectotipo de *Sporolithon irinae* (Maslov), comb. nov.

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

INTRODUCTION

This is the fourth contribution within the framework of the taxonomic revision of the taxa described by Maslov, a Russian author who worked from 1929 to 1973 in Silurian to Miocene sedimentary rocks from the vast geographic area of the former USSR (Bassi *et al.*, 2002). Previous contributions focused on the reassessment of *Solenomeris afonensis* Maslov, 1956 (Bassi, 2003), the reassessment of the corallinalean genera established by Maslov (Bassi *et al.*, 2005), and the re-examination of the species attributed to *Lithophyllum* Philippi, 1837 and *Melobesia* Lamouroux, 1812 by this author (Braga *et al.*, 2005).

The original diagnostic characters of many species and genera of fossil coralline algae are of weak or doubtful taxonomic significance. Names available in the literature have rarely been used by subsequent authors due to the lack of reliable definitions. New species (and genera) have been established ignoring previously described taxa, further contributing to the large number of existing species names (Aguirre & Braga, 2005). Recently, however, reassessments of the original collections of some fossil coralline taxa have been carried out in the context of modern taxonomic understanding (e.g. Rasser & Piller, 1994; Aguirre *et al.*, 1996; Aguirre & Braga, 1998; Basso *et al.*, 1998; Bassi *et al.*, 2000, 2005; Woelkerling *et al.*, 2002; Braga *et al.*, 2005).

The new taxa of fossil calcareous algae described by Maslov, who published most of his work in Russian monographs printed in the former USSR, have largely been ignored. Notwithstanding, they represent a large number of species (60 species and infraspecific taxa, Bassi *et al.*, 2002) and genus names that must be taken into consideration in any taxonomic work dealing with corallinalean algae.

Maslov described only five new species and infraspecific taxa within *Archaeolithamnium* (Bassi *et al.*, 2002). The primary aim of this work was to reassess the type collections of these five taxa originally placed in *Archaeolithothamnium* Rothpletz, 1891 (Maslov, 1936, 1956). The type material of *Archaeolithothamnium rude* var. *asiaticum* Maslov, 1936, however, has not been found.

Archaeolithothamnium Rothpletz, 1891 is an invalid name (see Moussavian & Kuss, 1990) that has been incorrectly used as a substitute for *Sporolithon* Heydrich, 1897. *Sporolithon* is a coralline genus mainly restricted to low latitudes (Johnson, 1963; Adey & Macintyre, 1973; Johansen, 1981), where it primarily lives in relatively deep water and cryptic sites (Adey, 1979, 1986). *Sporolithon* is the earliest recorded representative of modern Corallinales and first appears in Lower Cretaceous (Hautervian) reef deposits in Spain (Arias *et al.*, 1995). According to the data from literature surveys, the genus reached its greatest species richness in the Turonian-Coniacian, during the warmest period in the post-Palaeozoic history of the Earth. Since the Late Cretaceous, the species richness of *Sporolithon* has declined with small fluctuations, following the global temperature decrease recorded in the oceans by different palaeotemperature proxies (Aguirre *et al.*, 2000). Assessing the relationships of Maslov's species examined herein to the many other congeneric taxa described from the long standing geological record of *Sporolithon* is beyond the scope of the present study.

MATERIALS AND METHODS

Maslov's original material is only 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. Thin-section study was performed using light microscopy. Coralline-algal growth-form and anatomical terminology follows Woelkerling (1988), Braga *et al.* (1993), and Woelkerling *et al.* (1993). Cell and conceptacle dimensions follow Chamberlain *et al.* (1988).

SYSTEMATIC PALAEONTOLOGY

Order CORALLINALES Silva & Johansen, 1986

Family **Sporolithaceae** Verheij, 1993

The Corallinales is the only order of Rhodophyta in which most or all vegetative cell walls are impregnated with calcite (Silva & Johansen, 1986). Presently, three families with living representatives are recognised within the Corallinales: Corallinaceae, Hapalidiaceae, and Sporolithaceae (Harvey *et al.*, 2003). Verheij (1993) proposed a new family, Sporolithaceae, to separate *Sporolithon* from the rest of the Corallinales based on the cruciate cleavage of spores within tetrasporangia, which develop in tetrasporangial chambers surrounded by calcified paraphysis (filaments) instead of developing in conceptacles. Townsend *et al.* (1995) characterise the Sporolithaceae by "tetrasporangia that produce cruciately arranged spores and develop within calcified sporangial compartments".

Heydrichia Townsend, Chamberlain & Keats, 1994 was later established as a new genus of Sporolithaceae. It was separated from *Sporolithon* by having more than one stalk cell in each sporangial compartment and by the occurrence of cell filaments making up the sporangial compartment wall, among other features with very low preservation potential in fossil specimens, such as the restriction of spermatangial systems to the male conceptacle floor.

Representative recent accounts of living members of the Sporolithaceae have been published by Harvey *et al.* (2002, 2005).

Genus *Sporolithon* Heydrich, 1897

Sporolithon afonense (Maslov, 1956), comb. nov
Figs. 2a-d

Basionym: *Archaeolithothamnium afonensis* Maslov. Maslov, 1956, Fossil calcareous algae of USSR. *Trudy Instituta geologicheskih nauk Akademii Nauk SSSR* (in Russian), pp. 137-138, text-fig. 59a-b.

1962 *Archaeolithothamnium afonense* Maslov; Maslov, 43, text-fig. 18.

Holotype: Designated by Maslov (1956: 138), thin section 3504/3/2 (Fig. 1). Text-fig. 59b is a drawing of two sporangial compartments that can be identified in the largest plant fragment in this thin section.

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

Examination of the type collection: The holotype section includes a fragment of a small protuberance (3 mm long and 1.2 mm wide) with lateral lamellar branches. Other plant fragments consist of superimposed encrusting branches.

The plant has dorsiventral and monomerous organisation with a basal core of filaments oblique to the ventral side, curving upwards to become perpendicular to the thallus surface in the peripheral region. In the protuberance the filaments are radially arranged (Fig. 2c). Cells in the ventral core are squarish to trapezoidal in section, measuring 14 μm in length and 13-15 μm in diameter. The cells in the peripheral region are squarish to rectangular in section, measuring 14-21 μm in length and 13-14 μm in diameter. Cell fusions are common and cells of contiguous filaments are not laterally aligned. Dense micrite layers within the protuberance and branching thalli indicate old thallus surfaces subsequently overgrown by new filaments. Zonation of the peripheral region is generally weak. No epithallial cells have been recognised.

Reproductive structures consist of sporangial compartments (*sensu* Townsend *et al.*, 1995) grouped in sori and buried in the thallus. The number of compartments in each sorus is relatively small (up to 6) in the available section. Individual compartments are elliptical to ovoid in longitudinal section. They measure 65–80 μm in diameter and 95–115 μm in height. No distinct cells or cell layers occur at the base of compartments (Table 1). Sporangial compartments are separated by several filaments with no distinct cells (Fig. 2d). No structures attributable to gametangial conceptacles can be observed.

Remarks: The reproductive structures in the holotype are characteristic of sporangial plants of *Sporolithon* Heydrich, 1897 (Woelkerling, 1988, 1996; Townsend *et al.*, 1994). *Sporolithon* is the correct generic name for corallines included by many authors in *Archaeolithothamnium* Rothpletz, 1891, since this latter name was not validly published (Woelkerling, 1988; Moussavian & Kuss, 1990). The sporangial compartments in the type of *A. afonensis*

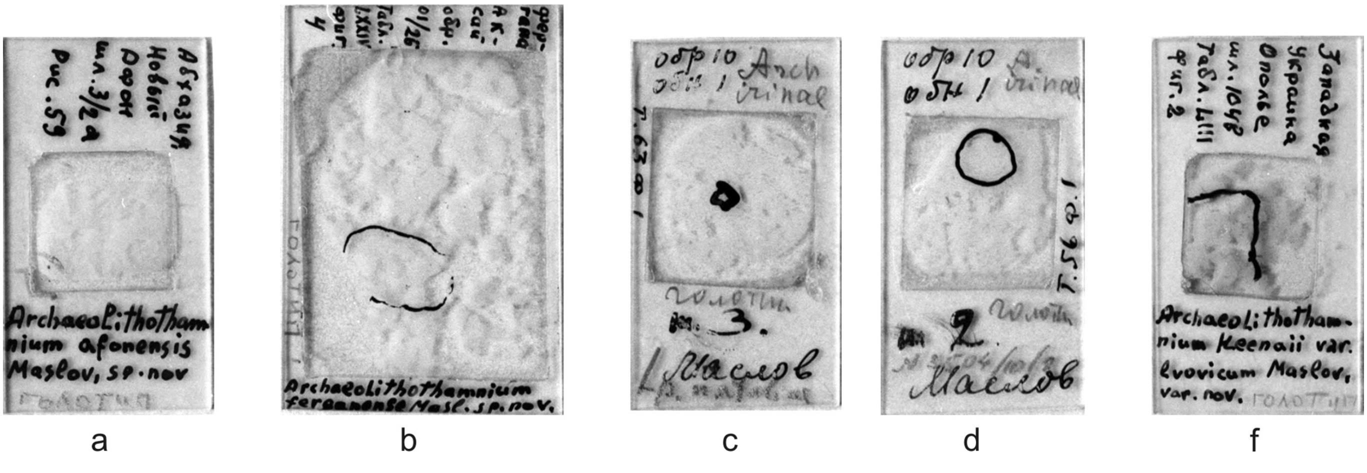

Figure 1. Thin sections from Maslov's collection at the Geological Institute, Russian Academy of Sciences, Moscow. **a**, *Archaeolithothamnium afonensis* Maslov, 1956; 3504/3/2, holotype. **b**, *Archaeolithothamnium ferganense*, Maslov, 1956; 1/26, holotype. **c**, **d**, *Archaeolithothamnium irinae*, Maslov, 1956; 3504/10/3; 3504/10/2, lectotype. **f**, *Archaeolithothamnium keenanii* var. *lvovicum* Maslov, 1956; 3504/1048, holotype.

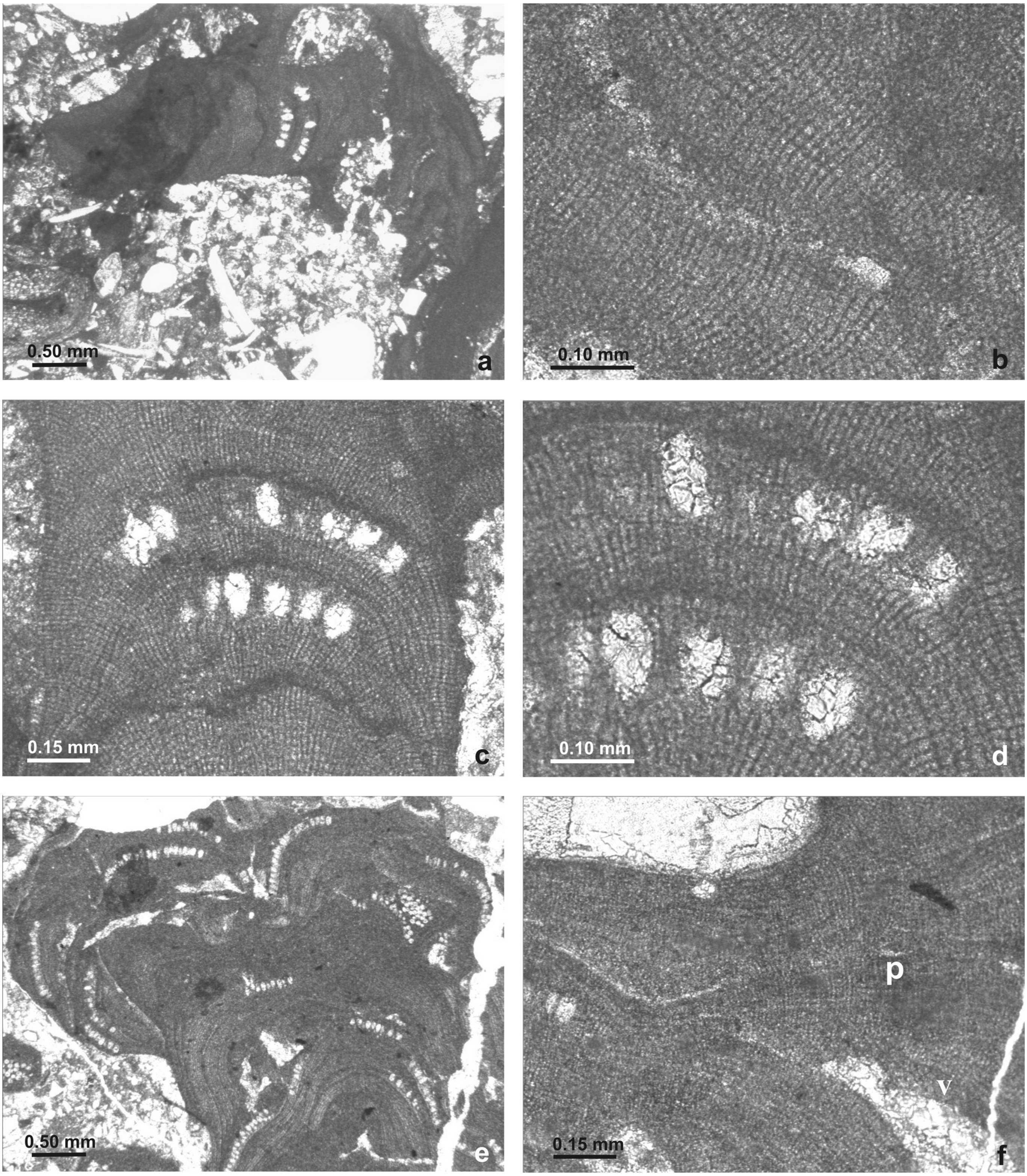

Figure 2. **a-d:** *Sporolithon afonense* (Maslov, 1956), comb. nov.; **a**, section of the holotype consisting of a fragment of a small protuberance with lateral lamellar branches; **b**, detail of the basal core of filaments that are oblique to the ventral side and curve upwards; **c-d**, details of sori of elliptical to ovoid sporangial compartments. **e-f:** *Sporolithon ferganense* (Maslov, 1956), comb. nov.; **e**, section of a nodule of lumpy thalli; **f**, cell filaments are oblique to the ventral surface (v) and curve upwards to become perpendicular to thallus surface in the peripheral region (p).

Species	**Compartment size (μm)**	**Basal layer of elongated cells**	**Number of observed compartments in section per sorus**	**Alignment of cells of adjacent filaments**
S. afonense (Maslov, 1956)	65-80/95-115	no	less than 10	no
S. ferganense (Maslov, 1956)	40-55/65-85	no	several tens	locally but not persistent
S. irinae (Maslov, 1956)	30-35/60-70	no	between 10 and 20	no
S. lvovicum (Maslov, 1956)	40-55/90-100	no	several tens	no

Table 1. Significant characters of the *Sporolithon* (*S.*) species examined in this study.

do not show any of the features diagnostic of *Heydrichia* Townsend, Chaberlain & Keats, 1994 such as more than one stalk cell and filaments at the wall of each sporangial compartment. The preservation potential of these features in fossil plants, however, is unknown. We therefore propose the new combination *Sporolithon afonense* (Maslov, 1956), comb. nov. for naming this species. Maslov (1956) considered this species similar to *A. megamiensis* Ishijima, 1933 except for its branching growth habit and the shape and distribution of sporangial compartments.

Sporolithon ferganense (Maslov, 1956), comb. nov.

Figs. 2e-f, 3a-c

Basionym: *Archaeolithothamnium ferganense* Maslov. Maslov, 1956, Fossil calcareous algae of USSR. *Trudy Instituta geologicheskih nauk Akademii Nauk SSSR* (in Russian), pp. 186-187, text-fig. 102, pl. 74 figs. 1-4.

1962 *Archaeolithothamnium ferganense* Maslov; Maslov, 44, text-fig. 19.

Holotype: Sample 1/26, designated by Maslov (1956: 187). A thin section cut from this sample, illustrated by Maslov (1956) in pl. 74 fig. 4, is the only material remaining from the original collection consisting of at least three algal nodules shown in pl. 74 figs. 1-3 (Fig. 1).

Age and locality: Eocene (Alayskiy stage); Fergana, Uzbekistan.

Examination of the type collection: The holotype is a nodule of lumpy thalli, with protuberances up to 4 mm long and 5 mm wide.

The thalli have dorsiventral and monomerous organisation. The cell filaments are oblique to the ventral surface and curve upwards to become perpendicular to the thallus surface in the peripheral region. The filaments are radially arranged in the protuberances (Fig. 3a). Cells are small and squarish, 10–15 μm in long and 10–15 μm in diameter. Cell fusions are common and cells of contiguous filaments may be laterally aligned, especially in the protuberances, but lateral cell alignment is not persistent. Changes in micrite density in cell walls produce weak zonation within the thalli. Epithallial cells have not been recognised.

The preserved reproductive structures are grouped sporangial compartments (*sensu* Townsend *et al.*, 1995). Sori protruded on the thallus surface while they were functional and were subsequently buried by new plant growth. They include a large number of compartments, more than 20 in some sorus sections. Individual compartments are elliptical to rectangular with rounded corners in longitudinal section. They measure 40–55 μm in diameter and 65–85 μm in height. A trapezoidal stalk cell can be observed in a few compartments but no distinct cell layer occurs at their base (Fig. 3c; Table 1). Sporangial compartments are separated by several filaments with no distinct cells. No structures attributable to gametangial conceptacles can be observed.

Remarks: The vegetative and reproductive features of the type of *Archaeolithothamnium ferganense* are characteristic of *Sporolithon* (see remarks on *S. afonense*). Therefore we propose the new combination *Sporolithon ferganense* (Maslov, 1956), comb. nov. for this species. Maslov (1956) separated this species from others of the genus by the smaller size of its cells and sporangial chambers and by the absence of cell-size zones within the thallus.

Sporolithon irinae (Maslov, 1956), comb. nov.

Figs. 3d-f, 4a-b

Basionym: *Archaeolithothamnium Irinae* Maslov. Maslov, 1956, Fossil calcareous algae of USSR. *Trudy Instituta geologicheskih nauk Akademii Nauk SSSR* (in Russian), pp. 153-154, text-fig. 76, pl. 56 figs. 1-2.

1962 *Archaeolithothamnium irinae* Maslov; Maslov, 44, text-fig. 20.

Lectotype: Here we select thin section 3504/10/2 as the lectotype of *A. irinae*. Maslov (1956: 154) designated thin section 3504/10/2 as the holotype. This thin section is labelled "holotype", probably by a curator of Maslov's collection and even the plate number (T. 56) is written in the margin (Fig. 1). The coralline plant illustrated by Maslov (1956) in pl. 56 figs. 1 and 2, however, occurs in another thin section (3504/10/3), also labelled "holotype", perhaps because it also includes the holotype of *Karpathia nataliae* (Maslov, 1956) Bassi, Braga, Zakrevskaya & Radionova, 2005. The only illustration identifiable as belonging to a plant in thin section 3504/10/2 is a drawing of a series of sporangial compartments in text-fig. 76α. Maslov (1956) did

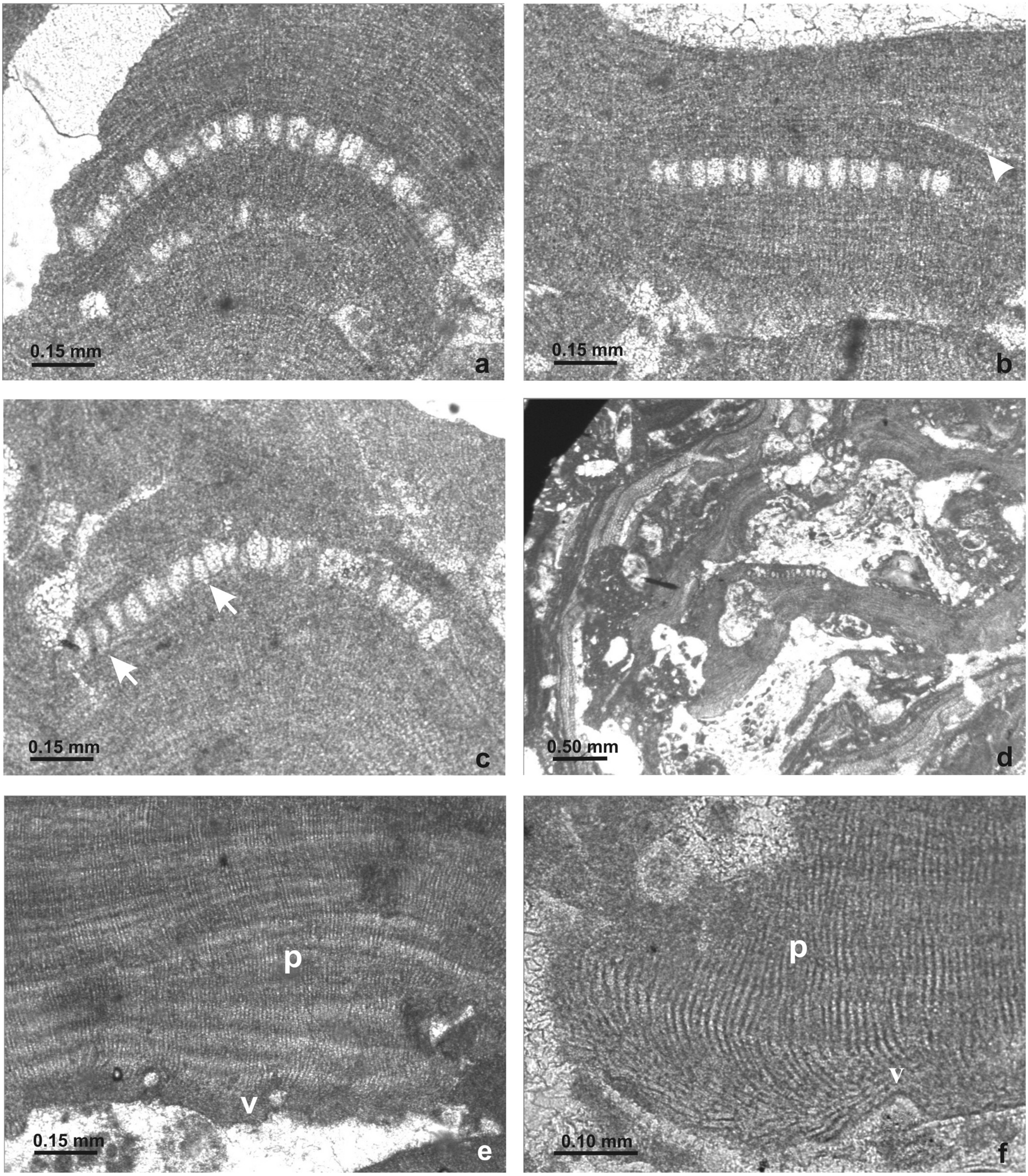

Figure 3. **a-c:** *Sporolithon ferganense* (Maslov, 1956), comb. nov.; **a-c**, sections of thalli with elliptical to rectangular sporangial compartments. Trapezoidal stalk cells (arrows) occur at the base of a few compartments; note in figure 3b that the sorus protruding on the thallus surface was subsequently buried by new plant growth (arrowhead). **d-f:** *Sporolithon irinae* (Maslov, 1956), comb. nov.; **d**, many encrusting plants attached to foraminiferal and other invertebrate tests; **e-f**, thallus sections showing a plumose ventral core in which cell filaments run parallel to the ventral surface (v) and curve upwards to become perpendicular to the dorsal surface in the peripheral region (p); note that walls separating adjacent filaments are well defined.

not clarify in the protologue of *A. irinae* whether the two thin sections (3504/10/2 and 3504/10/3) were cut from the same or from different samples, but the latter possibility seems more probable due to the different numbering. There are, therefore, validating illustrations probably based on more than one specimen. The type specimen was indicated by Maslov (1956: 154) but not identified among the validating illustrations and, according to Art. 9.13 of the ICBN (McNeill *et al.*, 2006), a lectotype must be designated.

Age and locality: Badenian, Miocene; Toltry, Gumenzy village, Ukraine.

Examination of the type collection: The two thin sections contain encrusting plants attached to foraminifers and other invertebrate tests.

The thalli have dorsiventral and monomerous organisation with a ventral plumose core in which the cell filaments run parallel to the ventral surface for a short distance and curve upwards while dividing to become perpendicular to the dorsal surface in the peripheral region (Figs. 3e-f). Cells in the core are rectangular in section, 14–25 μm long and 7–12 μm in diameter, whereas they are square and small in the peripheral region (7–10 μm long and 7–10 μm in diameter). Cell fusions are scarce and walls separating adjacent filaments are well defined. There is no lateral alignment of cells of adjacent filaments but weak zonation is created by slight changes in micrite density (darkness) of cell walls.

The reproductive structures are sporangial compartments grouped in sori. The best-preserved sorus protrudes on the thallus surface (Fig. 4a). Other sori were buried by subsequent growth of the thallus. Individual compartments are elliptical to ovoid in longitudinal section, 30–35 μm in diameter and 60–70 μm high. No distinct layer of elongated cells occurs at their base (Table 1). Trapezoidal stalk cells can be observed in a few compartments.

Remarks: The reproductive features of the type of *Archaeolithothamnium irinae* Maslov, 1956 are characteristic of *Sporolithon* (see remarks on *S. afonense*). We therefore propose the new combination *Sporolithon irinae* (Maslov, 1956), comb. nov. for this species name. In the protologue Maslov (1956) did not justify the description of *S. irinae* as a separate species.

Sporolithon lvovicum (Maslov, 1956), comb. nov.

Figs. 4c-f

Basionym: *Archaeolithothamnium keenanii* var. *lvovicum* Maslov. Maslov, 1956. Fossil calcareous algae of USSR. *Trudy Instituta geologicheskih nauk Akademii Nauk SSSR*, 160, pp. 151-152, pl. 53 fig. 2; pls. 54-55, text-fig. 75.

*	1956	*Archaeolithothamnium Keenanii* var. *lvovicum* n. var.; Maslov, 151-152, pl. 53 fig. 2; pls. 54-55, text-fig. 75.
non	1958	*Archaeolithothamnium keenanii* var. *veronensis* n. var.; Mastrorilli, 6, pl. 1 fig. 3.
?	1962	*A. keenanii* var. *lvovicum* Maslov; Maslov, 46-47, text-fig. 21.
	1973	*Archaeolithothamnium keenenii* var. *lvovicum* Masl.; Maslov, pl. 22 fig. 2.
non	1973	*Archaeolithothamnium pseudokeenanii* n. nom.; Mastrorilli, 250-251, pl. 3 fig. 3.
non	1985	*Archaeolithothamnium lvovicum* Maslov; Pisera, 100, pl. 17 fig. 1.
	1985	*Archaeolithothamnium lvovicum* Maslov; Pisera, 100, pl. 17 figs. 2-4.
	1988	*Archaeolithothamnium keenani* Howe; Studencki, 17, pl. 3 fig. 1; pl. 9 fig. 5.
	1989	*Archaeolithothamnium lvovicum* (Maslov) Pisera, 1985; Pisera & Studencki, 193-194, pl. 5 fig. 1b.
non	1994	*Sporolithon lvovicum* (Maslov); Bucur & Filipescu, pl. 2 fig. 2.

Holotype: Designated by Maslov (1956: 152), thin section 3504/1048 (Fig. 1), illustrated by Maslov in pl. 53 fig. 2, pl. 55, and text-fig. 75.

Age and locality: Badenian, Miocene; Opol'e, road between Lagodov and Sivorosch, western Ukraine.

Examination of the type collection: The only preserved material is the holotype, a thin section cut from one of the many algal nodules that Maslov studied from the type locality. Twelve of them appear in plate 54 (Maslov, 1956). The holotype is a lumpy plant about 1 cm across with protuberances up to 3.5 mm high and up to 4.0 mm wide (Figs. 4c-d). The plant has dorsiventral and monomerous organisation with a basal portion of filaments oblique to the ventral surface encrusted on other coralline plants. Away from the basal portion, the cell filaments curve upwards to become perpendicular to the thallus surface in the peripheral region or radially arranged within the protuberances. Cells are small and squarish (10–15 μm long and 10–15 μm in diameter). Cell fusions seem to be common and lateral alignment of cells of adjacent filaments is generally poorly defined. No epithallial cells were recognised.

The preserved reproductive structures are sporangial compartments grouped in large sori, concentrated in the protuberances. At their fertile stage, sori, including tens of sporangial compartments, slightly protruded on the thallus surface and were buried by renewed growth of the thallus. Individual compartments are elliptical to rectangular with rounded corners in longitudinal section, 40–55 μm in diameter and 90–100 μm in height. No distinct layer of elongated cells occurs at their base (Table 1). Trapezoidal stalk cells can be observed in some compartments (Fig. 4f).

Remarks: The occurrence of single stalk cells and the absence of peripheral filaments at the walls of sporangial compartments indicate that the type of *A. keeanii* var. *lvovicum* Maslov, 1956 belongs to *Sporolithon* Heydrich (see remarks in *S. afonensis*) and we propose the new combination *Sporolithon lvovicum*. Maslov (1956) distinguished this taxon from *A. keeanii* by its smaller thallus thickness and by the absence of the "a median hypothallium". The meaning of the latter term, not referred to in the original description of *A. keeanii* by Howe (1934) is unintelligible. The sporangial compartment dimensions of *Archaeolithothamnium keenanii* Howe are smaller that the ones

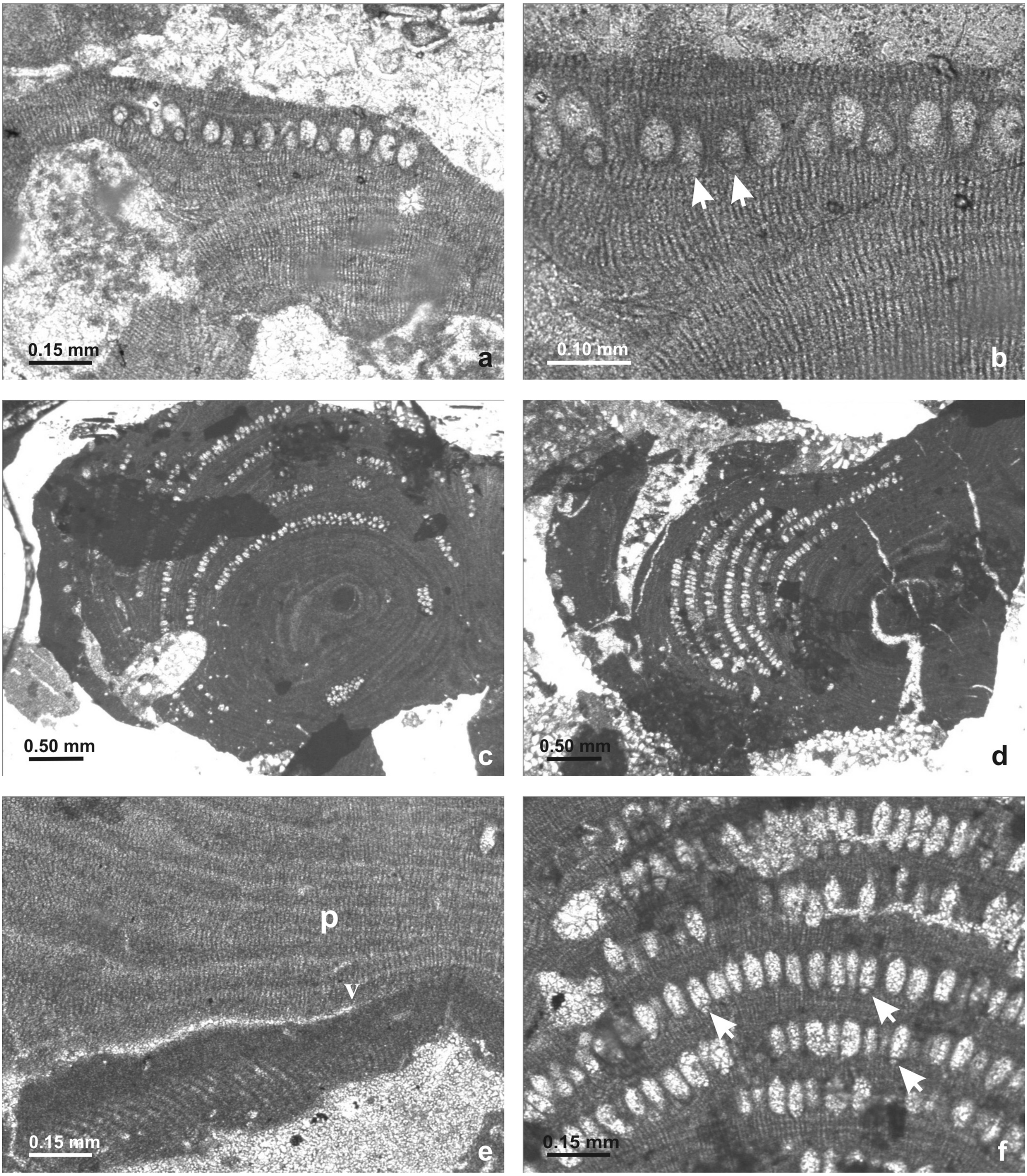

Figure 4. **a-b:** *Sporolithon irinae* (Maslov, 1956), comb. nov.; **a**, detail of figure 3d illustrating a preserved sorus protruding on the thallus surface; **b**, sections of sporangial compartments showing trapezoidal stalk cells (arrows). **c-f:** *Sporolithon lvovicum* (Maslov, 1956), comb. nov.; **c-d**, oblique (c) and longitudinal (d) sections of a lumpy plant; **e**, cell filaments in the ventral (v) and peripheral (p) regions; lateral alignment of cells is poorly defined; **f**, sori include tens of sporangial compartments; arrows indicate trapezoidal stalk cells.

in the type of Maslov's infraspecific name. In addition, the specimen illustrated by Howe (1934) of *A. keenanii* shows a well-defined lateral alignment of cells of adjacent filaments that does not occur in *S. keenanii* var. *lvovicum*. These features warrant the recognition of *S. lvovicum* as a separate species name as proposed by Pisera (1985, as *Archaeolithothamnium lvovicum*).

Bucur & Filipescu (1994) transferred *A. lvovicum* to the genus *Sporolithon* as one of the many species names included in a table (Bucur & Filipescu, 1994: 41, table 1) with no clear indication of the basionym. The new combination of these authors, therefore, is not validly published according to Art. 33.3 of the ICBN (McNeill *et al.*, 2006).

Mastrorilli (1973: 251) considered that *A. keenani* var. *lvovicum* Maslov, 1956 and *A. keenanii* var. *veronensis* Mastrorilli, 1958 possess similar morphometrical parameters (cell and sporangial-compartment dimensions) and included the two taxa in her new species *Archaeolithothamnium pseudokeenanii* Mastrorilli (1973: 250). No reasons for not using one of the two infraspecific names instead of proposing a new species name are given in the protologue of the latter species. However, the occurrence of a basal layer of elongated cells in the holotype of *A. pseudokeenanii* suggests that this taxon is not co-specific with *S. lvovicum* according to the diagnostic characters currently used in the species taxonomy of Sporolithaceae. The presence of such a basal layer of elongated cells also separates *A. keenanii* var. *veronensis* (Mastrorilli, 1958) from *S. lvovicum* (Table 1). The specimens ascribed to *lvovicum* and illustrated by Mastrorilli (1958: pl. 1 fig. 3; 1973: pl. 3 fig. 3), Pisera (1985: pl. 17 fig. 1), and Bucur & Filipescu (1994: pl. 2 fig. 2) show a clear basal layer of elongated cells below the compartments suggesting that they cannot be assigned to Maslov's species.

Studencki (1988) considered *A. keenanii* var. *lvovicum* and *A. pseudokeenanii* as heterotypic synonyms of *A. keenani* Howe, 1934 due to a lack of significant morphometric differences. By contrast, Pisera and Studencki (1989) separated *A. lvovicum* Maslov from *A. keenani* Howe based on differences in the shape and placement of sporangial compartments and for biogeographical and stratigraphic reasons. In the same paper, they attributed the specimens described by Studencki (1988) as *A. keenani* to *A. intermedium* Raineri, 1924.

Archaeolithothamnium rude var. *asiaticum* Maslov, 1936

* 1936 *Archaeolithothamnium rude* var. *asiaticum* Maslov, 119, pl. 1 figs. 1-3.
1956 *Archaeolithothamnium rude* var. *asiaticum* Maslov, 168.
1962 *Archaeolithothamnium rude* var. *asiaticum* Maslov, 50.

Remarks: No material associated with *Archaeolithothamnium rude* var. *asiaticum* Maslov, 1936 was found. The original pictures of Maslov (1936, pl. 1 figs. 1-3) show sporangial sori that would place this taxon in the family Sporolithaceae. Maslov (1936, 1956) describes the sporangial compartments as elongated forms, 100–120 μm in diameter and 160–200 μm in height, locally closely grouped. Maslov (1936, 1956) mentioned the smaller cells and the higher number of sporangial compartments as the characters separating the new infraspecific taxon from *A. rude* Lemoine, 1925. Maslov (1936) stated that he received two samples found in Sarmatian deposits of Kara-Tau, southern Kazakhstan. One of them originated from lower Sarmatian sediments near the Dzaprakty mountain.

CONCLUSIONS

After assessment of the four type collections of *Archaeolithothamnium* species described by Maslov (1956) housed in the Geological Institute at the Russian Academy of Sciences of Moscow, *A. afonensis*, *A. ferganense*, and *A. irinae* have been formally transferred to *Sporolithon* at species level, and a lectotype has been designated for *A. irinae*. *A. keenani* var. *lvovicum*, which had been raised to species rank by Pisera (1985) also has been transferred to *Sporolithon* at species level. The type of *A. rude* var. *asiaticum* has not been found and consequently formal assessment of this taxon has not been possible.

The status of these taxa as distinct species within *Sporolithon* requires further evaluation. The criteria used by Maslov to separate species of *Sporolithon* are different from those used to delimit species within Sporolithaceae in modern taxonomic practice (Table 1) and are of doubtful value in species separation.

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