Paleontological Journal, Vol. 36, No. 5, 2002, pp. 541–547. Translated from Paleontologicheskii Zhurnal, No. 5, 2002, pp. 100–105.

Lichenlike Fossils from the Givetian of Central Kazakhstan

A. L. Jurina* and V. A. Krassilov**

**Moscow State University, Vorob'evy gory, Moscow, 119899, Russia*
***Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya ul. 123, Moscow, 117997 Russia*
e-mail: vkras@paleo.ru
Received February 15, 2001

Abstract—A new genus, *Flabellitha* Krassilov et Jurina, gen. nov., is described based on leaflike flabellate fossils from the Givetian of central Kazakhstan. Microstructural characters suggest its affinity with foliose lichens. This is the first find of a Paleozoic representative of the group supposedly indicating a relatively early appearance of lichens.

INTRODUCTION

The members of the new genus described in the present article were originally assigned to *Flabellofolium elinae* Jur. et Put. from central Kazakhstan (Jurina and Putjatina, 2000). On the basis of elongated cuneate isolated leaves dissected into additional lobes, having what these authors believed to be poorly preserved and only in places visible dichotomous venation, they referred to these plant remains as a species of the formal genus *Flabellofolium*, a member of the group of Paleozoic plants with ginkgolike megaphylls.

The microstructural examination with the aid of a scanning electron microscope, by V.A. Krassilov at the Paleontological Institute of the Russian Academy of Sciences (PIN), did not discover any traces of vascular tissues or stomatal structures. On the contrary, the examination revealed certain structures that are not characteristic of higher plants. Additional data allow us to reinterpret the affinity of the discussed imprints and to consider them to be imprints more closely resembling lichen thalli.

SOME MORPHOLOGICAL FEATURES OF MODERN LICHENS

There are three general morphological groups of lichen thalli: (1) crustose thalli, usually closely adnated to the substrate; (2) foliose thalli, adhered to the substrate and mainly removable from it; and (3) fruticose thalli usually consisting of dissected branches or bands, connected to the substrate only by the base (Oksner, 1974; Trass and Golubkova, 1977).

The simplest thallus of foliose lichens, monophyllous thallus, consists of a solitary leaf plate, which is often emarginate or dissected into lobes. Polyphyllous foliose thalli are composed of several leaflike plates. Lichenologists consider foliose lichens to be more advanced in comparison with crustose lichens (Trass and Golubkova, 1977). The following four layers are usually distinguishable on cross sections of the thallus: the upper and lower cortical layers, algal layer, and the medullar layer. Foliose lichens do not all have lower cortex. The cortical layer is composed by a dense network of fungal hyphae forming a pseudotissue, the paraplectenchyma. In this layer, the tubular stereomic strands occur. The strands consist of sclerotized hyphae having a mechanical function. A loose tissue that forms a margin along the thallus periphery is discerned as the spongy paraplectenchyma. Swollen spherical cells containing oil substance are occasionally present on the cortical hyphae. The function of these cells is not entirely known. It has been hypothesized that the oils are used by lichen during the formation of apothecia or during the periods unfavorable for thallus development. The oils may also be excretes. In the algal layer, photosynthesis and accumulation of organic substances take place. This layer consists of algal cells, which are continuously or locally distributed among loose thin-walled hyphae. The main function of the medullar layer is the air conduction to the algal cells. The layer consists of loosely interwoven fungal hyphae.

GEOLOGICAL RECORD OF LICHENS

Most modern textbooks on general paleontology and paleobotany lack information concerning fossil lichens. Presently, the discovery of lichen geological history is at its very beginning. The time of the appearance and the origin of lichens are unknown. It was proposed that, in the Precambrian and Early Paleozoic, the land was inhabited by algae and lichens; however, no evidence of the lichen's presence was given. In the 19th century and early 20th century, lichen remains were very briefly described from supposed Paleozoic, Triassic, and Tertiary deposits. Pia (in Hirmer, 1937) reviewed such finds and dated the appearance of lichens as the Middle Paleogene or, tentatively, as far back as the Middle Carboniferous. He illustrated the stratigraphical succession by the example of three families: the Graphidaceae, known in the Quaternary and sup-

Explanation of Plate 10

Figs. 1–6. *Flabellitha elinae* (Jurina et Putjatina) Krassilov et Jurina, holotype MSU, no. 50/362: (1) fragment of the thallus, marginal zones with the spongy plectenchyma, SEM, ×20; (2) lobed foliose thallus, ×2; (3) groups and filaments of spheroids of the subcortical layer, SEM, ×1200; (4) striate surface of spheroids, SEM, ×4500; (5) spores in depressions of the cortical layer (arrows), SEM, ×400; (6) bicellular spores, SEM, ×1200; (7) filamentous structure of the algal layer with an envelope, a trichome emerges at the right end of the filament, SEM, ×1400.

posedly appearing in the Middle Cretaceous; the Cladoniaceae and Parmeliaceae, which were recorded beginning from the Middle Paleogene. However, the thallus morphology has not been studied in detail.

In the last two decades, paleobotanical material on lichens has been scrutinized in a range of studies. The criteria for the assignment of the oldest remains to lichens have been established. Thus, Taylor *et al.* (1997) proposed to treat as lichens the fossils that exhibit the presence of both symbionts. Moreover, the lichen thallus should differ from those of fungi and algae that do not form symbiotic organisms. We concur with the first statement proposed by Taylor stressing also the significance of microstructural features characteristic only of modern members of the group.

The finds of fossils assigned to the genus *Thuchomyces* in the Precambrian, series Witwatersrand of South Africa, are considered to be the oldest finds of lichens (Hallbauer *et al.*, 1977). According to the reconstruction proposed, the tubular thallus develops on a horizontal basal platform. The thallus structure is formed by hyphae similar in organization to those of modern fungi. Taylor *et al.* (1997) doubted that *Thuchomyces* belonged to lichens, since they believed that the symbiotic association was not substantiated. However, the original description of this genus included geochemical data indicating that *Thuchomyces* contained a phycobiont (Hallbauer *et al.*, 1977). Other data on presumable lichen finds from the Precambrian, for example, certain Ediacaran organisms (Retallack, 1994), are questionable.

The earliest proven lichens, in which symbiosis is well substantiated, are known from the Lower Devonian (Pragian) Rhynie Chert of Scotland and assigned to the genus *Winfrenatia* (Taylor *et al.*, 1997). The thallus of this lichen consists of horizontal layers of aseptate hyphae that form a three-dimensional netlike structure. The phytobiont is spherical coccoid cyanobacterial cells or clusters of cells. Reproduction is provided by endospores and soredia. Although the thallus organization of *Winfrenatia* does not resemble those of modern lichens, the evidence of symbiotic interaction between the components allow the authors to consider the genus *Winfrenatia* to be the first true lichen in the geological history.

Fossils with coriaceous phytoleims and a thick cuticle-like cover are known from the Lower Devonian. One of them, the genus *Spongiophyton*, has been interpreted as a possible lichen on the basis of new finds from the Lower Devonian of North America (Stein *et al.*, 1993). However, this hypothesis has not been supported by microstructural data.

In the later geological history (until the Eocene), reliable finds of lichens are not known. Lichen remains from the Eocene amber of the Baltic shores were described with various degree of detail (Caspary, 1906; Garty *et al.*, 1982; etc.). However, all these finds need to be reinterpreted and reexamined with the application of modern methods.

MATERIAL AND METHODS

The material of the present study includes two fragments of leaflike imprints. One of them is a subcrustation, a ferruginous film deposited under the covering layer (separated during decay) and showing the structure of inner tissues (Krassilov and Makulbekov, 1996). The paraplectenchymatous structure of the thallus with a spongy margin is visible under a small magnification of a stereoscopic microscope MBS-10. The imprint with the subcrustation (holotype) was washed with distilled water, placed on a stub, sprayed by gold, and studied with a scanning electron microscope CamScan. Herbarial specimens of modern lichens and fresh material collected by the authors were used for comparison.

The material described is housed at the Department of Paleontology of the Geological Faculty of Moscow State University (MSU), no. 50.

STRATIGRAPHIC OCCURRENCE

The material came from the Kossai locality, 50 km south of the village of Egendybulak (former Kuvsk) of the Karaganda Region. The locality was discovered in 1960 by the geologist E.M. Velikovskaya (Central Kazakhstan Expedition of MSU), who also found *Flabellitha* remains on tobacco-green fine-platy shales of the lower part of the Akbastau Formation. Other organic remains were not found in this locality. Additional samplings were not performed because the locality is hard-to-reach.

Stratigraphically, the Kossai locality is correlated with the plant-bearing section on the left bank of the Karagash River (Martynova and Uspenskii, 1971; text-fig. 21, section 3). Both sections belong to the marginal zone of the Dzhungar-Balkhash Region. The layers containing fossil flora were primarily considered to be the upper beds of the Givetian (Martynova and Uspenskii, 1971). Presently, these beds are included into the lower (Givetian) part of the Akbastau Formation (Mazarovich *et al.*, 1977). The age determination is confirmed by faunal remains characteristic of the *Spinocyrtia audacula* Brachyopod Zone of the Upper Givetian

Plate 10

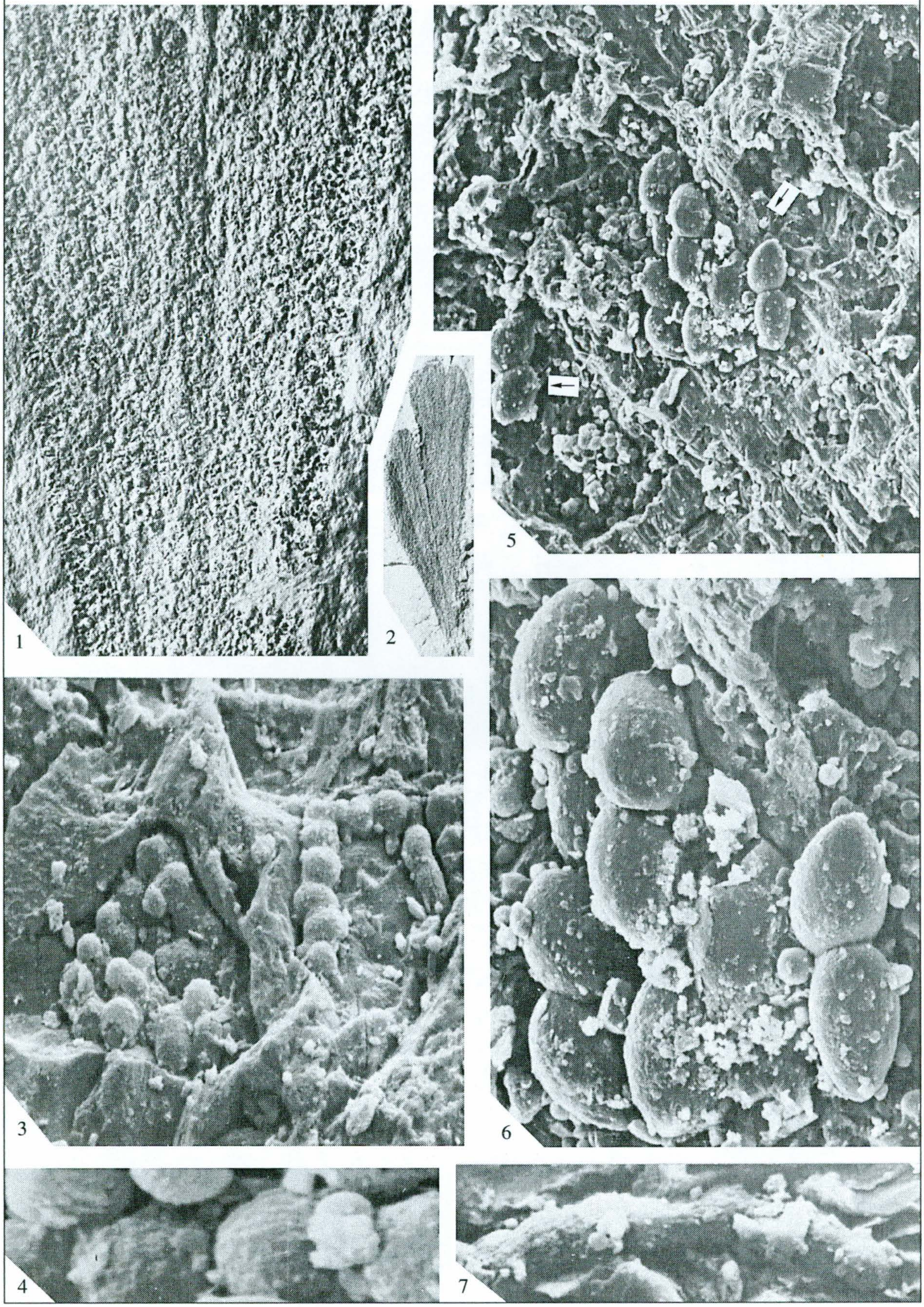
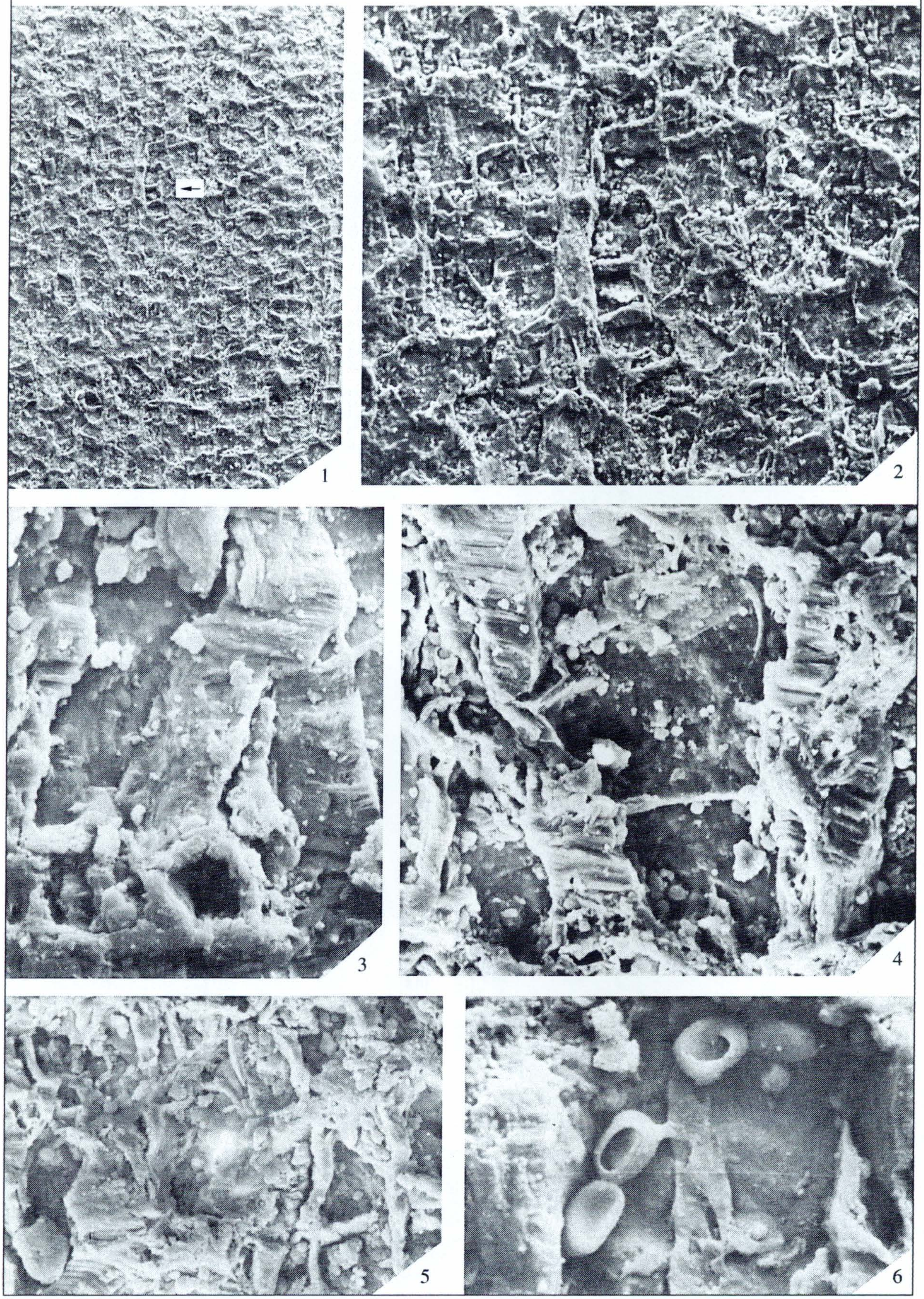


Plate 11



(Martynova, 1971, 1978). This zone is correlated with the *Lepidodendropsis kazachstanica* Floral Zone (Jurina, 1988), whose members were found in the lower part of the Akbastau Formation.

SYSTEMATIC PALEOBOTANY

Genus *Flabellitha* Krassilov et Jurina, gen. nov.

Etymology. From the Latin *flabellatus* (fan) and the first syllable of the Latin *thallus*.

Type species. *Flabellofolium elinae* Jurina et Putjatina, 2000, Givetian, lower part of the Akbastau Formation, Karaganda Region, Central Kazakhstan.

Diagnosis. Thallus foliose laminar, irregularly lobed, tuberculate. Cortex paraplectenchymatous, of broad tubular hyphae, with transversely striate walls, with marginal spongy zones and with longitudinal strands of thick-walled septate stereomic hyphae. Subcortical layer of thin hyphae containing spheroid cells in masses and beadlike chains. Apothecia inconspicuous and probably sunken. Spores two per ascus, large, bicellular, elongate–elliptical with pointed to obtuse ends.

Species composition. Type species.

Remarks. According to our interpretation, the main features of the described material, such as the paraplectenchymatous cortex, subcortical layer with spheroid cells, tubular hyphae, and large bicellular spores, are comparable with those of modern foliose lichens. However, there is little reason for performing comparison at genetic level, since the features usually used for generic systematics are impossible to reveal in fossil material. In particular, the morphology of fruiting bodies is insufficiently studied. Moreover, the outline of the Devonian thallus considerably differs from those of modern lichens and the hollow tubes forming the cortical layer are significantly thicker than hyphae of modern lichens. Among fossils, members of *Flabellofolium*, which have leaf plates with tubular cells, merit special attention (see Jurina and Putjatina, 2000 for the review), because they apparently do not belong to higher plants but need to be microstructurally examined for the comparison with the material described in the present study.

Flabellitha elinae (Jurina et Putjatina, 2000) Krassilov et Jurina, comb. nov.

Plate 10, figs. 1–7; Plate 11, figs. 1–6

Flabellofolium elinae: Jurina and Putjatina, 2000, p. 108, pl. 12, figs. 3 and 4.

Holotype. MSU, Geological Faculty, no. 50/362, Central Kazakhstan, Karaganda Region, Karkaralinsk District, near the Doumen Deposit, Kossai Mountain, Givetian Stage, lower part of the Akbastau Formation.

Description. Preserved regions of the thallus are flabellate, cuneate at the base, and asymmetrically dissected into two lobes (Pl. 10, fig. 1, 2). The visible width of the thallus in its broadest part is 8 mm; its length is 24 mm. The narrow cuneate lobes differ from each other by the width (3–4 mm and 6–8 mm, respectively). The outer side of the lobes is somewhat convex; the inner side is almost straight. A small notch at the apex of the lobes is supposedly an incipient dissection into additional lobes. A slitlike sinus between the lobes extends as a distinct fold over the undissected region of the thallus. Divergent folds and a fine striation extending in parallel to the folds are visible on the imprint of the surface. Numerous conical tubercles (0.2–0.3 mm in diameter) are scattered on the blade surface. Relatively large (0.5 mm) subspherical tubercles rarely occur among them.

One imprint is a subcrustation, a ferruginous film, deposited under the cortical layer and reproducing the morphology of its inner surface. A dense net of irregularly isodiametrical and transversely elongated angular or rounded meshes of about 40–60 μm wide is visible in SEM (Pl. 11, fig. 1). The net is formed by hollow, transversely rounded tubes of various thickness (on average 10–15 μm), and is interpreted as paraplectenchyma of the cortical layer. The longitudinal walls of the hyphae are transversely striated (Pl. 11, figs. 3, 4). Thick hyphae are occasionally connected by considerably thinner transverse anastomoses. Longitudinal strands up to 0.5 mm long are distinguishable amidst the uniform paraplectenchyma of the middle part of the thallus. The strands are composed of septate hyphae with thicker (40–50 μm) walls (Pl. 11, fig. 2). The transverse walls of the strands are sometimes split along the middle line. We describe the strands of short thick-walled rectangular cells as stereomic strands. Marginally, bands of denser spongy paraplectenchyma approximately 0.5 mm wide are distinguishable (Pl. 10, fig. 1).

In several cases, ellipsoidal smooth-walled emergences resembling hollow oil cells of extant lichens of about 10 μm long deviate from the thick cortical hyphae (Pl. 11, fig. 5).

Fairly thin (5–7 μm) hyphae of the subcortical layer forming a loose irregular network are preserved on the subcrustation of the inner surface of the cortical layer. Numerous rounded, rarely ellipsoidal spheroid cells about 5 μm in diameter are present in this layer. They are arranged in beadlike chains (Pl. 10, fig. 3) or irregular groups. In some cases, the chains of the spheroids

Explanation of Plate 11

Figs. 1–6. *Flabellitha elinae* (Jurina et Putjatina) Krassilov et Jurina, holotype MSU, no. 50/362, SEM: (1) fragment of paraplectenchyma of the cortical layer with a steroid (see arrow), ×60; (2) steroid strand, ×200; (3) transversely cut hollow hypha of the cortical layer, ×1000; (4) transversely striated hyphae of the cortical layer, connected by a thin bridge, ×700; (5) thin hyphae of the subcortical layer, ×400; (6) hollow oil cells, attached to a hypha of the subcortical layer, ×1400.

are partially covered by tubular envelopes and project out of the latter at the ends (Pl. 10, fig. 7). At high magnification, longitudinal striae or rows of tubercles, presumable remains of dried slime, are visible on the surface of the spheroids (Pl. 10, fig. 4).

Structures of the inner cortical layer show irregular depressions of about 200 μm wide surrounded by an undulated discontinous border. Two of these depressions contain spores, arranged by two in parallel rows. The spores are bicellular, smooth, elongate, approximately 40 μm long and 12 μm wide, pointed or at one end obtuse, with a constriction 8 μm wide. The cells of the spores are oval, slightly nonuniform (19 and 22 μm long), isolated from each other by an oblique septum (Pl. 10, figs. 5, 6).

O c c u r r e n c e. Givetian Stage of Central Kazakhstan.

M a t e r i a l. Holotype and one more imprint from the same locality.

DISCUSSION

The assignment of the remains to extinct lichens is based on the comparison with modern lichens in a number of microstructural features. The wrinkled surface of the imprint with microscopic tubercles resembles the surface with cephalodia of *Peltigera* and other modern lichens. The cortical layer, preserved as a subcrustation, is shown to be a paraplectenchyma formed by hollow septate tubes of different thickness. The transverse striation indicates thick slime walls, which are known in many lichenized fungi, characterized by much thicker hyphae than nonlichenized fungi. When observed under a SEM, the cortical hyphae of the modern Parmeliaceae have transverse striation, similar to that of fossil lichens, although it is less regular. Stereomic strands of the same type as those of *Flabellitha* are quite common in the Parmeliaceae and Umbilicariaceae. In particular, even such details as the splitting of transverse septa is registered. Anastomosing hyphae (connected by thin strands), which are observed in *Flabellitha*, are also described in the genus *Peltigera* and related modern genera of foliose lichens. Oil cells, which are present on the cortical hyphae, are a characteristic feature of the lichen mycobiont observed in some species of modern *Parmelia* (Oksner, 1974).

To date, it is impossible to provide an unequivocal interpretation of the spheroid cells of the subcortical layer. They are comparable to nonorganic structures, in particular, to colloidal globuli and to spheroid medullar cells, occasionally present in *Parmelia* (Rassadina, 1971). However, with reference to the dimensions and configuration of filamentous colonies having a partially preserved envelope and the trichome projecting out of the latter, these spheroids are especially similar to the most common phycobionts of modern lichens, i.e., cyanophytes and green algae, such as *Anabaena*, *Stigonema*, *Coccomyxa*, etc. Dried slime frequently forms parallel striation on the surface of algal spheroid cells, as in fossil spheroids.

Available information on the fruit bodies of *Flabellitha* is very poor and vague. We have not found distinct apothecia. We can only hypothesize that the depressions in the cortical layer correspond to sunken apothecia. However, this assumption is confirmed by the find of ascospores having typically lichen morphology. The bicellular spores are arranged in rows, retaining the configuration of asci; the walls of the latter are not preserved. It is notable that the destruction of thin walls of asci before the dissemination of spores is known in modern lichens (Bailey and Garrett, 1968).

The absence of a number of diagnostic characters hampers the taxonomic assignment of the genus *Flabellitha* among lichens. Such characters as the apothecium morphology, phycobiont nature, and thallus anatomy are taken into consideration for the differentiation of higher taxa of this group (Oksner, 1974; Trass and Golubkova, 1977). Considering all the data available, the new genus is most similar to modern members of the families Parmeliaceae, Peltigeraceae, and Nephromataceae. These families include large foliose lichens with emarginate-lobed and differentiated thalli; in some cases, the lower cortical layer is absent. In particular, the genus *Solorina* Ach. appears to be the closest modern analogue, having small lobed thalli, coarse cortical paraplectenchyma, and sunken apothecia with a narrow interrupted exciple and mostly bicellular spores, which in *S. bispora* Nyl. develop by two per ascus (Savich, 1975). This species has larger spores (approximately 90 × 40 μm) than the fossil lichen described in this paper. The spores dimensions of other species of this genus are similar to those of the fossil lichen, e.g., 40 × 20 μm in *S. platycarpa* Hue. The phycobionts of *Solorina* are either *Nostoc* or the green alga *Coccomyxa* with small slime-covered spheroid or elliptical cells.

A remark by Oksner (1974) about preferable development of oil cells in calciphilic lichens is important with reference to the growing conditions of *Flabellitha*. The remains of *Flabellitha* are preserved on the ferruginous surface of calcareous argillite (Shcherbakova, Geological Faculty, MSU, personal communication), and the appendages of the hyphae of the cortical layer are comparable to oil cells of modern calciphilic lichens.

CONCLUSION

Lichens or similar organisms are recorded in the Givetian flora for the first time. Their significance in the Devonian and older ecosystems has not yet been revealed. The genus *Flabellitha* is tentatively assigned to foliose lichens, since morphologically similar forms occur in this group, namely, among the modern Parmeliaceae and Peltigeraceae.

The finding of Givetian lichenlike fossil, which was primarily treated as a higher plant with ginkgolike leaves, indicates the necessity of revision of similar flabellate Devonian fossils. Special attention should be paid to the members of the genus *Flabellifolium* having either tracheid-like cells or tubes. Such specimens should be revised with the aid of a SEM.

ACKNOWLEDGMENTS

The study was partially supported by the Russian Foundation for Basic Research, project no. 98-04-49010 and the Federal Program "Integration," project no. C-0050/2000.

REFERENCES

Bailey, R.H. and Garrett, N.M., Studies on Discharge of Ascospore from Lichen Apothecia, *Lichenologist*, 1968, vol. 4, pp. 68–78.

Caspary, R., Die Flora des Bernsteines und anderer Fossiler Harze des ostpreufsischen Tertiärs, *Abh. Preuß. Geol. Landes., N.F.*, 1906, vol. 4.

Garty, J., Giele, C., and Krumbein, W.E., On the Occurrence of Pyrite in a Lichen-like Inclusion in Eocene Amber (Baltic), *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 1982, vol. 39, nos. 1/2, pp. 139–147.

Hallbauer, D.K., Jahns, H.M., and Beltmann, H.A., Morphological and Anatomical Observations on Some Precambrian Plants from the Witwatersrand, South Africa, *Geol. Rundschau.*, 1977, vol. 66, no. 2, pp. 477–491.

Hirmer, M., *Handbuch der Paläobotanik*, Berlin–München, 1927.

Jurina, A.L., Flora of the Middle and Late Devonian of Northern Eurasia, *Tr. Paleontol. Inst. Akad. Nauk SSSR* (Moscow), 1988, vol. 227, pp. 1–176.

Jurina, A.L. and Putiatina, O.N., Revision of the Genus *Flabellofolium* Stone, 1973 (Group of Paleozoic Plants with Ginkgo-like Megaphylls) and the First Findings of Its Givetian Members in Central Kazakhstan, *Paleontol. Zh.*, 2000, no. 3, pp. 103–110.

Krassilov, V.A. and Makulbekov, N.M., Subcrustations of Plants, *Paleontol. Zh.*, 1996, no. 2, pp. 125–128.

Martynova, M.V., Material on the Faunal Characteristics and Stratigraphy of the Givetian Stage of Central Kazakhstan, *Byull. Mosk. O–va Ispyt. Prir., Otd. Geol.*, 1971, vol. 46, no. 2, pp. 73–82.

Martynova, M.V., The Boundary between the Upper and Middle Devonian in Central Kazakhstan Based on Biostratigraphic Data, *Tezisy soobshchenii po biostratigrafii pogranichnykh sloev nizhnego i srednego devona SSSR na polevoi sessii Mezhdunarodnoi podkomissii po stratigrafii devona (15–25 avg. 1978)* (Abstracts on Biostratigraphy of Boundary Beds of the Upper and Middle Devonian of the USSR, Field Session of Int. Subcomm. Devonian Stratigr., Aug. 15–25, 1978), Leningrad: Vses. Geol. Inst., 1978, pp. 48–49.

Martynova, M.V. and Uspenskii, E.P., The Middle and Upper Series of the Devonian System, in *Materialy po geologii Tsentral'nogo Kazakhstana* (Data on the Geology of Central Kazakhstan), vol. 9: *Geologiya i metallogeniya vostochnoi chasti Tokrauskoi vpadiny i Yugo-Zapadnogo Chingiza* (Geology and Metallogeny of the Central Part of the Tokraus Depression and Southwestern Chingiz), Moscow: Mosk. Gos. Univ., 1971, pp. 55–71.

Mazarovich, O.A., Malinovskaya, S.P., Martynova, M.V., *et al.*, To the Regional Stratigraphic Chart of the Devonian of Central Kazakhstan, in *Geologiya i poleznye iskopaemye Tsentral'nogo Kazakhstana* (Geology and Minerals of Central Kazakhstan), Moscow: Nauka, 1977, pp. 116–131.

Oksner, A.N., *Opredelitel' lishainikov SSSR* (Key to Lichens of the USSR), Leningrad: Nauka, 1974, issue 2.

Rassadina, K.A., The Parmelliaceae, in *Lishainiki SSSR* (Lichens of the USSR), Leningrad: Nauka, 1971, pp. 282–386.

Retallack, G.J., Were the Ediacaran Fossils Lichens?, *Palaeobiology*, 1994, vol. 20, pp. 523–544.

Savich, V.P., The Genus *Solarina* Ach., in *Lishainiki SSSR* (Lichens of the USSR), Leningrad: Nauka, 1975, pp. 175–181.

Stein, W.E., Harmon, G.D., and Hueber, F.M., Spongiophyton from the Lower Devonian of North America Reinterpreted as a Lichen, *Am. J. Bot.*, 1993, vol. 80, no. 6 (Abstracts), p. 93.

Taylor, T.N., Hass, H., and Kerp, H., A Cyanolichen from the Lower Devonian Rhynie Chert, *Am. J. Bot.*, 1997, no. 7, pp. 992–1004.

Trass, Kh.Kh. and Golubkova, N.S., *Zhizn' rastenii* (Life of Plants), vol. 3: *Vodorosli, Lishainiki* (Algae and Lichens), Gollerbakh, M.M., Ed., Moscow: Prosveshchenie, 1977.