

# The First Finding of Gasteromycetes in the Cretaceous of Mongolia

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**Abstract**—The first Cretaceous find of Gasteromycetes comes from the Maastrichtian dinosaur beds of the Nemegt Basin, southern Gobi. A small group of fruiting bodies was found on the ferruginous surface of light gray clays containing abundant plant debris. Cretaceous fungal remains resemble *Geastrum* Pers., but differ in the irregular splitting of the exoperidium (a half of the exoperidium remains entire), a relatively small gleba indicating an early opening of the exoperidium, and larger spores. On account of these distinctions, a new genus, *Geastroidea* Krassilov gen. nov. is established. Mycelial films around the fruiting bodies might contribute to soil building on levee deposits. This find indicates that saprophytic fungi played a certain role in Cretaceous dinosaur ecosystems.

*Key word:* Gasteromycetes, Cretaceous, Mongolia.

## INTRODUCTION

The geological history of basidiomycetes is poorly understood. One of the most important groups, Gasteromycetes, has not been registered in pre-Miocene deposits. The sole find from the Oligocene, initially assigned to the Gasteromycetes (Coccherell, 1908), was later assigned to higher plants (Tiffney, 1981). Correspondingly, our data on Cretaceous Gasteromycetes are of interest for better insight into the evolutionary history of this group.

The material comes from Maastrichtian deposits of the Nemegt Basin (southern Gobi), which are known by abundant remains of dinosaurs and other vertebrates (Maleev, 1974; Rozhdestvenskii, 1974; Barsbold, 1985; Alifanov, 2000), freshwater mollusks (Martinson, 1982), charophytes (Kyansel-Romashkina, 1982), and aquatic and terrestrial higher plants (Krassilov and Makulbekov, 1995). The thickness of the Nemegt Formation is about 140 m. Its lower part consists of gravelly sands with interlayers of siltstones and clays; the upper part is composed of alternating sands and siltstones. Dinosaurs and turtles were collected at seven consecutive levels (Gradzinski *et al.*, 1968). Most plant remains come from the sand/shale member directly underlying the lower dinosaur bed, approximately 25 m above the base of the formation.

The fungal remains were found in the Tsagan-Khushu locality, situated 7 km west of Naran-Bulak. The locality is confined to a small outlier of variegated Maastrichtian deposits about 50 m thick. The lower part of the section includes a member of gray and dark gray clays containing fine plant debris. Numerous fruits of

aquatic plants resembling the family Lemnaceae were previously described from this locality (Krassilov and Makulbekov, 1995).

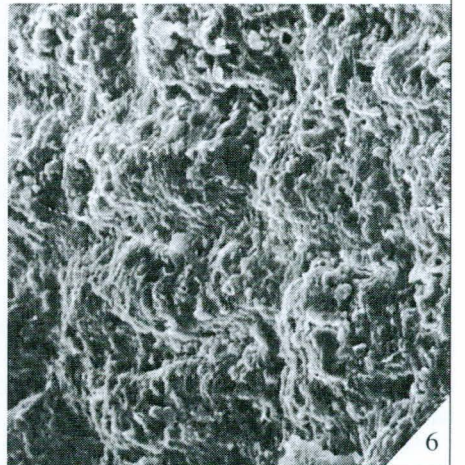
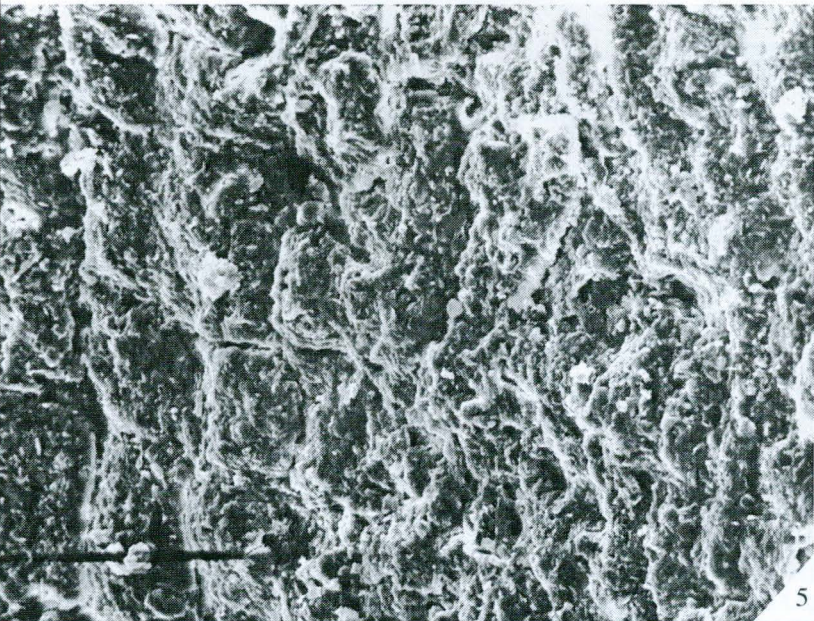
The new find extends the knowledge of fossil fungi and introduces a new element to the functioning of dinosaurian ecosystems. The majority of extant Gasteromycetes are soil saprophytes, playing an important role in the carbon cycle. Since their Cretaceous members are now proved to be essentially similar to extant forms, they might have performed a similar function in the dinosaurian ecosystems.

## MATERIAL AND METHODS

The material consists of impressions of open fruiting bodies, partly incrustated with a ferruginous film. The fruiting bodies are preserved on the surface of light gray silty clay with abundant plant debris. Several slightly undulate bedding planes, covered with the remains of root systems of higher plants and fine debris, are distinguishable in the plant-bearing bed 25 mm thick.

Small fragments of a fruiting body were picked off the rock matrix and placed on a standard stub for scanning electron microscopic (SEM) studies.

The plane beds with fungal fruiting bodies also contain thin films of dense interlacing fungal hyphae. Microscopically, the surface of these films appears verrucate or scaly because of peeling (Pl. 12, fig. 6). These structures are comparable to mycelial films of extant gasteromycetes. Moreover, the surface shows linear cords of the same consistency, which are similar to remains of horizontal roots of aquatic or semiaquatic



## Explanation of Plate 12

**Figs. 1–6.** The gasteromycete *Geastroidea lobata* Krassilov, gen. et sp. nov. from the Upper Cretaceous of Mongolia: (1) fruiting bodies on the surface of a silty clay with plant debris,  $\times 2$ ; (2) fruiting body with exoperidium opened by irregular lobes,  $\times 4$ ; (3) central part of a fruiting body, note the head (endoperidium) with a pore surrounded by the peristome (light contour), a scaly part of the exoperidium forming a fringe around the head, and the radial striation (rows of pseudoparenchymous cells) on the lobes of exoperidium,  $\times 6$ ; (4) a spore on the scaly entire part of the exoperidium, SEM,  $\times 1400$ ; (5) cells of pseudoparenchymous layer of the exoperidium with remnants of the fibrous layer, SEM,  $\times 250$ ; (6) mycelial film consisting of dense interlacing hyphae preserved around fruiting bodies, SEM,  $\times 280$ .

higher plants. These structures may represent mycelial cords of gasteromycetes, which are only superficially similar to plant roots. The fruiting bodies and surrounding mycelial films are light brown or yellow to light orange because of ferrugination.

The fungi apparently grew on the surface of levee deposits with abundant plant debris. The ferruginous bedding plane and the bleaching of the underlying clay to the depth of 1–2 mm suggest the initial stage of soil formation. Gasteromycetes possibly played a certain role in this process. However, a mature soil profile had not yet been formed on the fresh alluvium.

Extant Gasteromycetes include forest fungi, growing in the leaf litter under the forest canopy, and forms of open areas, growing on the meadow and steppe soils. The angiocarpic fruiting body covered by the peridium can develop in either subterranean or surficial conditions. The peridium opens at a certain developmental stage, either early in development, as in the Phallales, Hysterangiales, and other orders, or after complete spore maturation, as in the Melanogastrales. The basidium-bearing part of the fruiting body (gleba) is characterized by several developmental types of basidium and specialized hyphae related to the basidia. To date, such specialized hyphae have not been recognized in a fossil state. We link the Cretaceous remains under description with the family Geasteraceae, which is characterized by a double-layered peridium. The latter includes a relatively thick exoperidium split into lobes and a thin membranous endoperidium covering the gleba and opening as a single or several apical pores; occasionally, the latter is split together with the exoperidium. The overwhelming majority of gasteromycetes are saprophytes. One of the best known genera of this family, the Earthstar, comprises over 50 species, occurring on all the continents.

The comparison with extant gasteromycetes shows a considerable similarity between the Cretaceous form under study and the earthstar species *Geastrum nanum* Pers., *G. campestre* Morg., *G. floriforme* Vitt., and *G. minimum* Schw., growing in open landscapes (Sosin, 1973). They have relatively small fruiting bodies (10–30 mm) dehiscing by unequal lobes and developing in dense groups (in particular, *G. campestre* Morg. growing in groups on sandy soils and solitary in forest litter). Analogously, the Cretaceous species might have developed in dry open landscapes, which agrees with the concept of the supposedly open landscapes of the dinosaurian ecosystems (Krassilov, 1981).

## SYSTEMATIC PALEONTOLOGY

Genus *Geastroidea* Krassilov, gen. nov.

**Etymology.** From the generic name *Geastrum* Pers.

**Type species.** *Geastroidea lobata* sp. nov. from Upper Cretaceous (Maastrichtian) deposits of southern Gobi, Mongolia.

**Diagnosis.** Fruiting bodies angiocarpic, with exoperidium split into few irregular lobes. Innermost layer of exoperidium pseudoparenchymous, with radiating rows of elongate cells. Outermost layer of exoperidium scaly. Entire part of exoperidium forming scaly fringe around endoperidium. Head relatively small, sessile, rounded conical, truncate. Endoperidium scarious and opening by apical ostiole bordered by low peristome.

**Comparison.** The fossil is an angiocarpic fruiting body with a double-layered cover, a characteristic feature of the Gasteromycetes. The external layer (exoperidium) dehisces by lobes, exposing a head (gleba, covered with endoperidium) with a conspicuous apical pore bordered by a prominent ridge (peristome). These characters allow us to assign the fossil fruiting bodies to the family Geasteraceae. The most similar extant genus of the family is the earthstar (*Geastrum* Pers.). Species of this genus differ in the mode of dehiscence of the exoperidium, the shape of the head (sessile or pedicellate), the morphology of gleba and peristome, dimensions, color, and the surface sculpture of spores. The fossil form in question is especially similar to small surficial Earthstars growing in groups, with a sessile head and a low peristome, and lacking a clear areola. There is a general similarity between the remains described and such extant species as *G. saccatum* Fr., *G. indicum* (Klotzsch) St. Rauschert, *G. pseudolimbatum* Hollós (with a funnel-like entire part of the exoperidium), and some others (Sosin, 1973; Pilót, 1958).

However, there are also considerable differences from extant earthstars. The exoperidium of the Cretaceous form splits into three lobes, one of which exceeds two others in width, occupying about half of the circumference. Such a dehiscence pattern of the exoperidium is unknown in extant earthstars. Although their lobes vary in width, they are symmetrically arranged and at least four in number (more often about ten lobes). In addition, the Cretaceous form differs in a disproportional small head, indicating an early opening of the fruiting body that is atypical of *Geastrum* and the

Melanogastrales in general. Even in Miocene *G. tepexensis* Magallón-Puebla et Cevallos-Ferriz (1993), fruiting bodies are of approximately the same size and dehisced in 10 symmetrical lobes, the head was considerably larger (13 mm). A distinctive feature of the Cretaceous form is relatively large spores (supposing that the spores found attached to the peridium actually belong to this fungus). These differences allow us to describe the newly found Cretaceous gasteromycete as a new genus.

*Geastroidea lobata* Krassilov, sp. nov.

Plate 12, figs. 1–6

**E t y m o l o g y.** From the Latin *lobatus* (lobed).

**H o l o t y p e.** PIN, no. 3958/1-16, Tsagan-Ushu, Nemegt Basin, southern Gobi; Upper Cretaceous, Maastrichtian, Nemegt Formation.

**D i a g n o s i s.** Species of a monotypic genus.

**D e s c r i p t i o n.** An open fruiting body about 25 mm in diameter and fragments of two more fruiting bodies are preserved; apparently, they form a dense surficial group (Pl. 12, fig. 1). The exoperidium is split into three unequal lobes; their tips are immersed in the rock matrix and, apparently, curved to raise the head above the ground. Two lobes are widely cuneate, their maximal width in the distal part is 5 mm and 10 mm. The third is broader (13 mm), rounded elliptical in outline, and has two narrow basal ruptures extending for one third of the length (Pl. 12, fig. 2).

Under a SEM, the impression covered by a fine ferruginous incrusting film shows a pseudoparenchymous layer of radiating tetragonal and wedge-shaped longitudinally elongated cells. The cells are 100–150 µm long and about 55 µm wide. This layer is separated from the upper scaly layer by a slitlike hollow, which obviously corresponds to a nonpreserved middle fibrous layer. SEM also revealed fibrous structures adjacent to the incrustation of the pseudoparenchymous layer, which could be remnants of the middle layer (Pl. 12, fig. 5). The entire part of the exoperidium forms a shallow cup-shaped 2-mm-wide fringe around the head, which consists of a single scaly layer.

The head is small relative to the unfolded exoperidium, but distinct due to its dark brown color against the light yellow incrustation of exoperidium (Pl. 12, fig. 2), sessile, rounded conical, flattened, irregularly elliptic with uneven margin, 3 mm wide, and about 2 mm high. In the center, there is a relatively large elliptical pore (1.3 × 1 mm) bordered by a slightly elevated ridge (peristome) of uneven thickness. The weakly defined radial furrows diverge from the peristome. They apparently correspond to ruptures of the endoperidium. The head surface (endoperidium) is finely verrucate.

Under a SEM, spores, possibly released through ruptures of the endoperidium, are seen on the scaly fringe of the head. The spores are elliptical, smooth, and vary in size, with the greatest diameter 10 µm long.

Isolated lobes of exoperidium, showing the same layers as those of the holotype, are the only remains of two other fruiting bodies of the group.

**M a t e r i a l.** Holotype.

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