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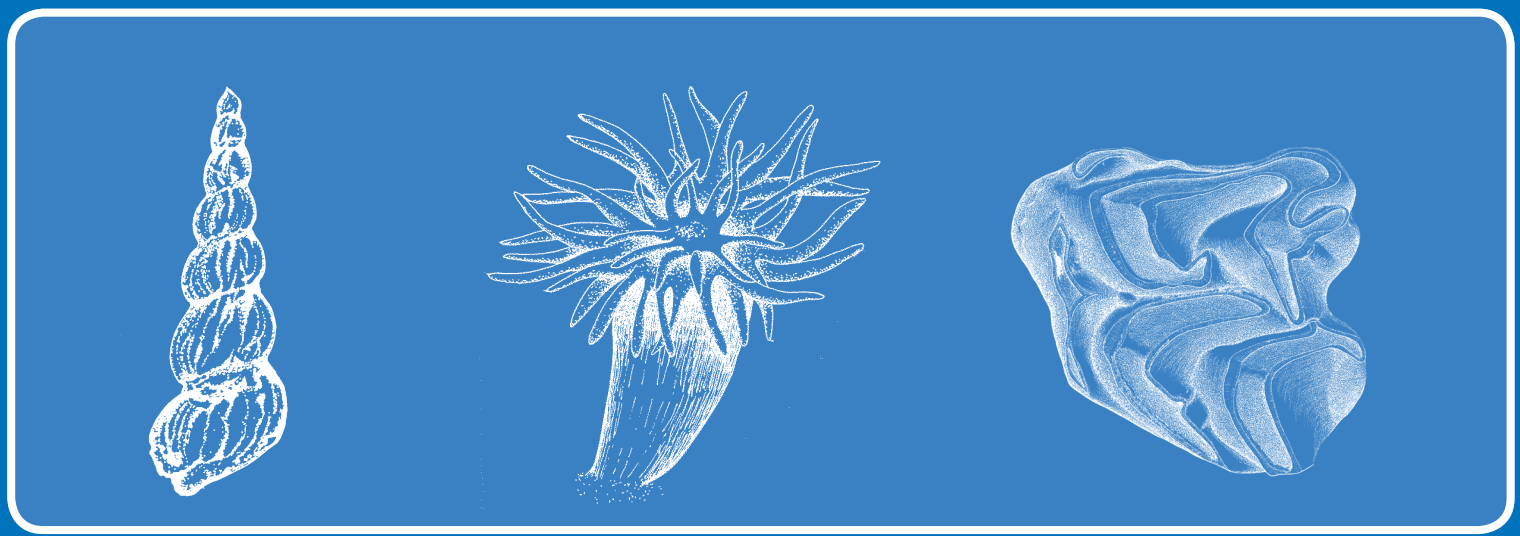

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Cover illustrations: (from left to right) Shell of the gastropod *Loxonema regium* De Koninck from the Carboniferous of Belgium (redrawn from De Koninck 1881); Solitary coral *Caninia* sp. from the Carboniferous of England (redrawn from Ramsbottom in McKerrow 1978); Tooth of the rare ruminant *Orygotherium escheri* von Meyer from the Miocene of Germany (after Rössner & Mörs 2001). **Back cover:** Atrium of the Munich Palaeontological Museum, view from the main entrance.

Umschlagbilder: (von links nach rechts) Gehäuse der Schnecke *Loxonema regium* De Koninck aus dem Karbon von Belgien (neu gezeichnet nach De Koninck 1881); Solitärkoralle *Caninia* sp. aus dem Karbon von England (neu gezeichnet nach Ramsbottom in McKerrow 1978); Zahn des seltenen Wiederkäuers *Orygotherium escheri* von Meyer aus dem Miozän von Deutschland (nach Rössner & Mörs 2001). **Rückseite:** Lichthof des Paläontologischen Museums München, Blick vom Haupteingang.

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Aracistrobus, an enigmatic non-araceous fossil from the Eurasian Oligocene and Miocene

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Abstract

Putative infructescences of Araceae described as *Aracistrobus* Nikitin ex Dorofeev (*A. dravertii* Nikitin ex Dorofeev) from the Upper Oligocene of western Siberia and Lower-Middle Miocene of European Russia and Germany have nothing to do with the Araceae because they differ in morphology and inner structure from the fruits of extant representatives of that family. The fossils are ovoid bodies of woody texture with honeycomb outer sculpture that are attached laterally (in one case alternately) to the sides and top of flattened axes. No seed remains have been recovered from the irregularly-disposed elongate surface cavities. The inner tissue is filamentous, partly fibrous or parenchymatous. Small leaf fragments with preserved cuticle suggesting willow or poplar leaf remains have been found attached to one body. The true nature of these bodies remains elusive. They recall fungi or lichens, but differ from these organisms in tissue structure. Another, although unlikely explanation considers these objects as galls produced by an unknown insect.

Key words: Enigmatic fossils, Tertiary, Fungi

Zusammenfassung

Vermeintliche Fruchstände von Araceae, die als *Aracistrobus* Nikitin ex Dorofeev (*A. dravertii* Nikitin ex Dorofeev) vom Oberoligozän Westsibiriens und Unter- bis Mittelmiozän vom europäischen Russland sowie aus Deutschland beschrieben wurden, haben nichts zu tun mit Araceae. Sie unterscheiden sich in der Morphologie und inneren Struktur von Früchten der lebenden Vertreter dieser Familie. Die untersuchten Reste sind eiförmige Körper von einer holzigen Textur mit honigwabenähnlicher äußerer Skulptur, die seitlich (in einem Fall alternativ) an den Seiten und der Spitze von flachen Achsen sich befinden. Es wurden keine Samenreste in den unregelmäßig angeordneten länglichen Vertiefungen der Oberfläche gefunden. Ihr inneres Gewebe ist fadenförmig, teilweise faserig oder schichtförmig. Kleine Blattfragmente mit erhaltener Kutikula legen Weiden- oder Pappel-Blattreste nahe und wurden zusammen verbunden an einem Körper gefunden. Die echte Natur dieser Körper verbleibt rätselhaft. Sie erinnern an Pilze oder Flechten, unterscheiden sich aber in der Struktur der Gewebe. Eine andere Erklärung erscheint unwahrscheinlich diese Objekte als Gallen von unbekannten Insekten zu betrachten.

Schlüsselwörter: rätselhafte Fossilien, Tertiär, Pilze

1. Introduction

The naming of plant fossils with doubtful affinities is a risky procedure, especially if a name is given that is suggestive of a certain relationship. This has happened several times in the family Araceae. A number of late Mesozoic and Cenozoic fossils have historically been attributed to the aroids and have been given scientific names suggestive of that biological affinity. However, subsequent detailed re-investigation of these fossils showed that many in fact are non-araceous (see Mayo et al. 1997; Wilde et al. 2005; Kvaček & Wilde 2006).

In this paper we revisit a set of intriguing fossils that were originally interpreted as infructescences of Araceae and named *Aracistrobus dravertii* Nikitin ex Dorofeev. Gregor & Bogner (1989) rejected the proposed affinities of these fossils with the Araceae, and re-interpreted the specimens as central bodies of *Platanus* infructescences devoid of fruitlets. We disagree with this interpretation, and offer an alternative view based on detailed comparisons of the material with other fossil and living organisms, and extensive discussions with several colleagues. The interpretation as *Platanus* infructescences by Gregor & Bogner (1989) was based on misidentified material.

2. Material and Methods

The type material of *Aracistrobus dravertii* Nikitin ex Dorofeev was collected by Dravert at the village of Ekaterinskoe on the Abrosimovka River, a right tributary of the Irtysh near the Tara Mountains in western Siberia, and studied (but not published) by Nikitin (at present missing *teste* Dorofeev 1957). Only one specimen from the original set of specimens

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has been illustrated [i.e. KRYSHTOFOVICH & BORSUK 1939, as *Spirematospermum wetzleri* (HEER) M. CHANDLER]. Subsequently discovered topotypical specimens by K. S. AFANASEV from the same layers and spots, and published as *Aracistrobus dravertii* by DOROFEEV (1957, 1963), have been borrowed from the collections of the Komarov Botanical Institute, RAS, St. Petersburg, and re-studied for the present paper (courtesy of D. V. GROMYKO, St. Petersburg). The fossils, which are fully carbonized, very tough and woody, were obtained by sieving sandy rocks for carpological material. We were given permission by the curators to try maceration. However, maceration in SCHULZE's solution, with successive rising in 5 % KOH, did not yield any resistant tissue. By treatment with the less aggressive disinfection and bleach agent "SAVO" (commercial Eau-de-Javelle) the fragments turned pale and became soft. Through mechanical preparation, small particles were transferred to microscope slides, rinsed in distilled water, and embedded in glycerol. Cell structure became recognizable by pressing the cover glass.

The photographic documentation was made with a COOLPIX 4500 camera, partly under a dissecting microscope; anatomical structure was observed and documented with an OLYMPUS biological microscope. The slides will be transferred to the collections of the Komarov Institute of Botany, RAS, St. Petersburg, after the study is completed.

Comparable fossils from the Miocene of Poland assigned to *Scindapsus lusaticus* CZECZOTT & SKIRGIEŁŁO (1967) have also been studied (courtesy R. KOWALSKI, Warsaw). One specimen (coll. Muzeum Ziemi, Warsaw, No. 899, pro parte), although very similar in surface view, is preserved as an impression in ironstone, and thus does not allow preparation of inner tissue. It most likely represents fruits of *Magnolia* (Magnoliaceae), but certainly does not belong to the Araceae (No. 899). The other superficially similar specimen from the Warsaw collection (No. 452) does not look araceous, and is here regarded as indeterminable. The remaining material of *Aracistrobus*, namely from the Miocene of Tambov (DOROFEEV 1988) and NW Saxony (MAI & WALTHER 1991; MAI 2000) has not been included in this study.

Another putative aroid infructescence, described and figured by PALAMAREV (1964: 136, pl. 10, fig. 3) as *Araceaecarpum* sp., comes from the Oligocene of the Pirin Basin, Bulgaria. This fossil has been suggested to be related to *Aracistrobus* (according to MAI 2000). Unfortunately, the specimen cannot be traced in the collection (D. IVANOV, Sofia, personal communication Nov. 2006). According to the illustration, however, it may represent a piece of wood covered by rounded perithecia of *Rosellinites* (cf. HIRMER 1927, fig. 106, as *Sphaerites areolata* FRESEN. & MEYER).

3. Taxonomy

Aracistrobus P.A. NIKITIN ex P.I. DOROF.

Aracistrobus dravertii P.A. NIKITIN ex P.I. DOROF.
Figs 1–12

1939 *Spirematospermum wetzleri* (HEER) M. CHANDLER – KRYSHTOFOVICH & BORSUK, p. 380, pl. 4, fig. 5

1957 *Aracistrobus dravertii* P.A. NIKITIN – DOROFEEV, p. 301, pl. 3, figs 1–3

1963 *Aracistrobus dravertii* P.A. NIKITIN – DOROFEEV, p. 135, pl. 17, figs 1–3

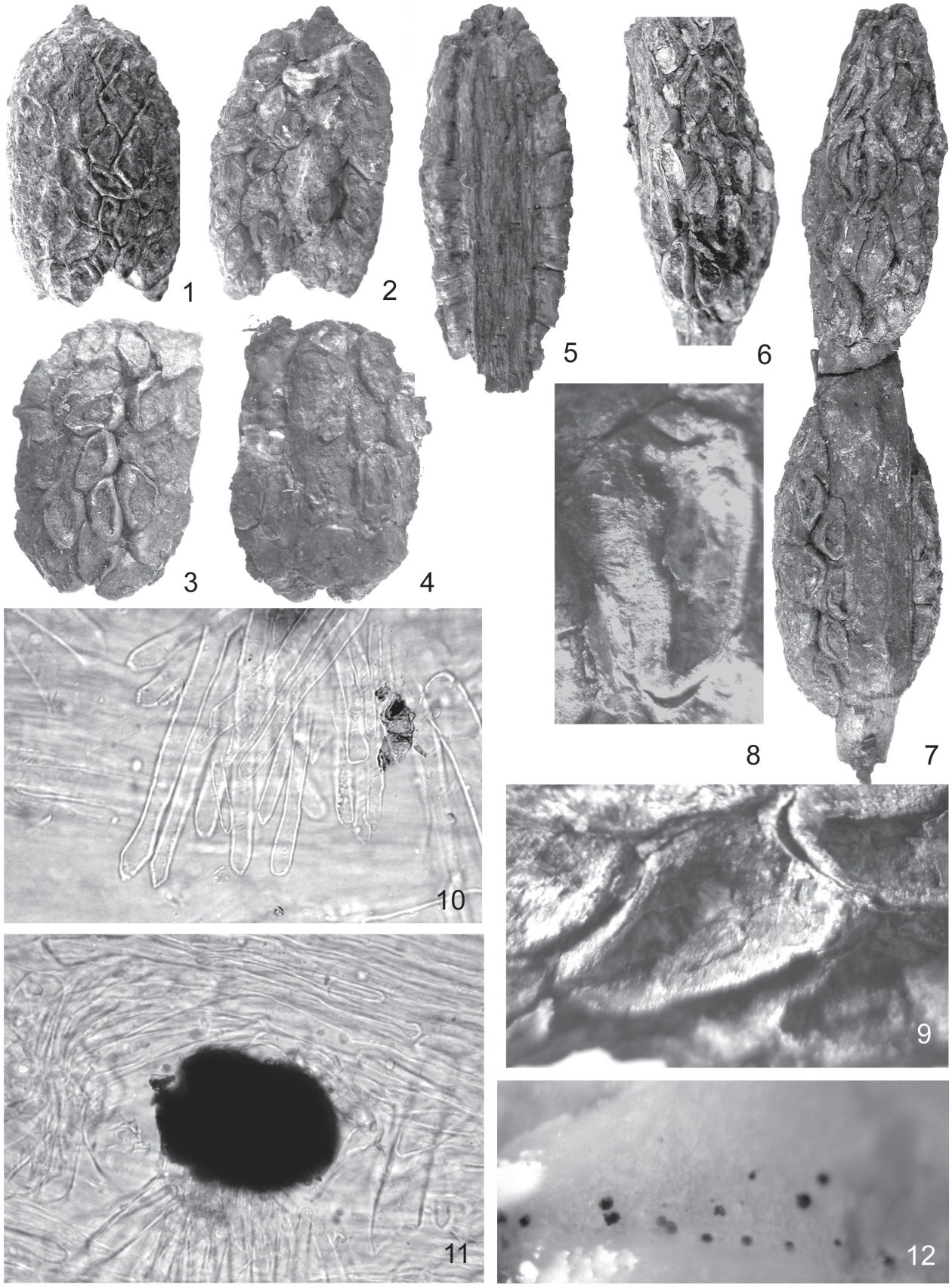
1991 *Aracistrobus dravertii* P.A. NIKITIN – MAI & WALTHER, p. 138, pl. 17, figs 43, 44

2000 *Aracistrobus dravertii* P.A. NIKITIN – MAI, p. 48, pl. 21, fig. 12.

The first description and illustration of the fossils in question was published by KRYSHTOFOVICH & BORSUK (1939), who misinterpreted them as capsule fruits of *Spirematospermum wetzleri* (HEER) M. CHANDLER. This misinterpretation becomes particularly clear if the illustration in KRYSHTOFOVICH & BORSUK (1939: pl. 4, fig. 5) is compared with the abundant fossils of *Spirematospermum*, an extinct representative of Zingiberales, illustrated in a recent paper by FISCHER et al. (2009). The error was recognized by DOROFEEV (1957), who validated the genus *Aracistrobus* in a generico-specifica diagnosis and provided a first short description of the species [in Russian]: „In the collection are many spadices recalling those of aroids. They represent thickened axes 3–4 cm long and 0.8–1.2 cm thick on which densely spaced and touching each other are compressed-saucer-shaped placentas, in which seeds once occurred. In some spadices the axis continues from the apex, representing axes of male inflorescences, like in living aroids (Acoreae). Seeds are not preserved. In the matrix a single aroid seed of *Epipremnum ornatum* of the Monsteroideae, has been recovered, although in other Tertiary deposits in Western Siberia abundant seeds of several species of *Aracispermum*, described by P. A. NIKITIN and allied to Acoreae occurred." *Aracispermum* does not belong to the Araceae as the name suggests, but rather to the Zingiberales.

Later DOROFEEV (1963: 135) provided a more detailed description [in Russian]: "Spadices one-sided, 1–2 on an axis, if two present than they are orientated on opposite sides. Axes primarily cylindrical, obviously composed of loose tissue, compressed due to fossilization, 3.5–7.0 mm wide, longitudinally scratched by thin veins. Spadices 3.2–5.4 × 1.7–2.0 cm, elongate oval, originally convex, due to fossilization compressed, by lateral sides passing on the opposite side. Fruits in number of 30–40 in each spadix, compressed saucer-shaped, on apices cross-cut, sections boat-shaped. Fruit walls thick, coriaceous, compressed into continuous folds. Seeds not recovered in any spadix."

We here confirm most features described based on the material from Ekatirenskoe (DOROFEEV 1963) that we have re-studied, with the exception of the terms "spadix" and "fruits". The somewhat flattened narrow ellipsoid bodies (Figs 1–7) vary considerably in length, i.e. from 62 mm (KRYSHTOFOVICH & BORSUK 1939: pl. 4, fig. 5) to 31 mm, and consistently cover one side of flattened axes. The stalks are compressed, almost entirely flat, varying in the width from 5 to 9 mm, parallel-sided throughout the attachment of each body. The stalks are always broken off immediately below, and firmly coalescent with the bodies throughout their length. Only in one case are two bodies attached to the same axis, ca. 5 mm apart, the upper of which is typically more slender and attached to the surface opposite that of the lower one (Fig. 7). In another case, the body is terminal, and slightly overgrows the rounded tip



Figures 1–12: *Aracistrobus dravertii* P.A. Nikitin ex P.I. Dorof., Ekaterinskoe, Upper Oligocene (coll. Komarov Botanical Institute, RAS, St. Petersburg). **(1–2)** Flattened body viewed from both sides, showing the sculpture on the outer surface; note irregular orientation of pits; ×2. **(3–4)** A similar, detached body with larger pits viewed from both sides; note a small remain of the stalk attached to the reverse side of the body; ×2. **(5)** Terminal elliptical body attached to the top of a stalk; ×2. **(6–7)** Reverse side and a full specimen bearing two alternate bodies attached oppositely to a stalk; ×2. **(8–9)** Details of pits; ×10. **(10, 11)** Inner structure of wall of pits, showing ends of filaments and a dark body (?disseminule) within tissue; × 400. **(12)** Distribution of dark bodies within tissue shown in Figure 11; × 50.

of the axis (Fig. 5). The lateral attachment of the bodies is a characteristic feature of *Aracistrobus dravertii*. None of the specimen indicates that the axis penetrates through the body. The surface of the bodies consists of cavities arranged in a honeycomb manner. The pits are hollow, hardly more than 3 mm deep, mostly elongate but varying in shape from almost rounded to narrow elongate or slit-like, typically 2–3 × 5–6 mm in size (Figs 8, 9). They are usually oriented longitudinally or obliquely, but may sometimes also be oriented perpendicularly to the axis. The walls are woody and finely parallel-striated. No other structural details are preserved. The interior (Fig. 10) consists of thin-walled tissue composed of partly dense fibrous tightly condensed filaments 100–300 µm long and 5–15 µm in diameter, and partly of isometric flattened cells. In the deeper parts of the pits, darker bodies, ca. 50–100 µm across, adhered (or were included in) the walls (Figs 11, 12). Remains of vascular bundles have not been observed. In one sample, a leaf fragment adhering to, or wedged between, the pits yielded the cuticle structure. The indistinctly striate adaxial cuticle reflects small wavy-walled cells, ca. 12–25 µm in diameter, lacking trichome bases, while the thicker and finely grained abaxial cuticle reflects similar, slightly larger non-modified cells, each 20–35 µm in diameter, and shows irregularly orientated brachyparacytic stomata. The guard cell pairs are narrow elliptical in the level of the cuticle, ca. 18–25 µm long, and are accompanied by wide parallel subsidiary cells, which are not always regularly distributed. This epidermal pattern is characteristic of some species of willows (*Salix*). We were unable to confirm resin canals in axes reported by Mai (in Mai & Walther 1991; Mai 2000) in the material from the Miocene of Saxony. The surface sculpture of the bodies is partly abraded and the pits are less distinct.

4. Discussion

Nikitin (*teste* Dorofeev 1963) believed that the specimens represent spadices of unknown fossil Araceae. Dorofeev (1957: 301) suggested that the apical continuation above some of the bodies may represent "axes of the male inflorescence similar to those seen in the living aroids (*Acoreae*)". *Epipremnum* (Araceae) and *Acorus* (Acoraceae) have uniform spadices with bisexual flowers, naked in *Epipremnum* and with a perigone in *Acorus*, but there are no male inflorescences as suggested by Dorofeev. Both Nikitin and Dorofeev were uncertain with regard to the aracean affinities of the fossils. Dorofeev (1963, 1988) discussed a possible relationship with *Epipremnum* and *Rhaphidophora*. This interpretation was accepted by Mai (in Mai & Walther 1991; Mai 2000), who also mentioned yellowish secretory elements in the axis.

In our opinion, the lateral position and overall variable morphology of the bodies and pits rule out affinities with the Araceae. The bodies adhere to the axes in full length, and vary in size in a similar way as surface stromata of some Ascomycetes. As a result, it is possible that the fossils represent plant remains infected by a fungus, which produced fruiting bodies on the host. Pyrenomycetes differ from perithecia in the rounded form. On the other hand, some members of the Rhytismatales produce boat-shaped hysterothecia that open by a longitudinal slit. The recovered cuticle suggests that the host plant might have been a species of *Salix*. However, specialists in mycology were unable to suggest a similar fungus that would produce this type of stromatal bodies. An alternative interpretation views the bodies as galls produced by insects. However, according to several entomologists, galls of similar composition and form are unknown today.

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