ISSN 0031-0301, Paleontological Journal, 2021, Vol. 55, No. 1, pp. 105–110. © Pleiades Publishing, Ltd., 2021.
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The First Record of the Rust Fungus (Pucciniales) Spores from Middle Eocene Sakhalinian Amber

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Received December 29, 2019; revised February 19, 2020; accepted March 21, 2020

Abstract—Fungus spores resembling teliospores of the genus *Nyssopsora* (Pucciniales) were found in a sample of Sakhalinian amber. Morphological features of the spores in the examined amber sample in general correspond to description of teliospores of the extant species *Nyssopsora trevesiae* parasitizing host plants of the Araliaceae, *Trevesia sundaica* in Java and Sumatra and *Brassaiopsis ciliata* in Southern China. It can be assumed that the plant on which those teliospores formed most likely belongs to the *Trevesia–Brassaiopsis* group. Extant species of these genera are characteristic of the undergrowth in humid forests from the Himalayas to Indonesia, which supports paleofaunistic data on rather warm and humid climate of Sakhalinian amber forest.

Keywords: *Nyssopsora trevesiae*, teliospores, Araliaceae, Naibuchi Formation, Sakhalinian amber

DOI: 10.1134/S0031030121010135

INTRODUCTION

In 1972, an expedition of the Paleontological Institute of the USSR Academy of Sciences collected a large collection of amber in the vicinity of Starodubskoye village on the eastern coast of southern Sakhalin, in which 838 specimens of insects were found (Zherikhin, 1978). An issue on the age of Sakhalinian amber has long been controversial. Based on indirect data, V.V. Zherikhin (1978) determined it over a wide range—from the Paleocene (Danian, 62–65.5 Ma) to the middle Eocene (42–47 Ma). Following geological and paleobotanical data, T.M. Kodrul (1999), convincingly substantiated the middle Eocene age of the Naibuchi Formation, in which Sakhalinian amber was found in situ.

For a long time, Sakhalinian amber has not been specifically studied; suffice it to say that the first spider, beetle and ichneumonoid wasp from Sakhalinian amber were only recently described (Marusik et al., 2018; Kazantsev, Perkovsky, 2019; Davidian et al., 2021). Recent expanded search for amber inclusions in the collections of the PIN RAS, commenced by E.E. Perkovsky and continued by V.V. Martynov (Slavyansk, Ukraine) almost doubled the number of known inclusions. The most interesting findings, in addition to those mentioned above, include the most ancient encyrtids (Simutnik, 2014, 2015), the oldest myrmicine ant of the extant genus (Radchenko, Perkovsky, 2016), the oldest Asian pedogenetic gall midge (Fedotova, Perkovsky, 2016), the first cicadellid from Asian Cenozoic ambers (Dietrich, Perkovsky, 2019). Fossil plants from Sakhalinian amber, namely mosses, were also described for the first time (Ignatov, Perkovsky, 2013). This article reports a rust fungus from the studied biota.

MATERIAL AND METHODS

The spores described in the article originate from the sample PIN no. 3387/973 (syninclusion—female Chironomidae) collected in Starodubskoye village in 1972 and stored in the collection of the Borissiak Paleontological Institute, RAS (PIN). Photos were taken with an Olympus C41 transmitted light microscope (10× and 20× lenses), with additional illumination from above with a Motic fiber optic illuminator, with an Infinity 2 digital camera.

RESULTS

The fungal spores in the studied sample were found to be morphologically very similar to the teliospores of representatives of the genus *Nyssopsora* Arthur (Pucciniales). They are embedded in the amber sample as a rather dense group of seven spores. No trace of the substrate on which they formed can be seen. Each spore consists of 3 cells; of them, the basal one is slightly larger than each of the other two which are both the apical cells. The contours resemble almost equilateral triangles with rounded corners, slightly constricted at the septa (Plate 12, Figs. 1–3; see inset). Spores are colored, but translucent, so that the septa are clearly visible. Spore sizes vary within 33–38 × 34–37 μm. Pedicels of teliospores are not observed. The outer walls of all cells are covered with numerous simple appendages up to 6–7 μm long, some of which are hooked at the apex (Plate 12, Figs. 2, 3). Some appendages were apparently torn off by the flow of resin and the spores are surrounded by a halo of debris.

DISCUSSION

Rust fungi (Pucciniales) is a group of obligate parasites of vascular plants, comprising about 7800 modern species (Kirk et al., 2008) that are characterized by complex morphology and ontogenesis: five types of sporulation follow each other in strict sequence, and many species require two unrelated hosts to complete their life cycle. A number of rusts are causative agents of dangerous diseases of cultivated plants. Such features of these pathogenic fungi support the significant interest of mycologists in their study. To date, a wealth of factual material has been accumulated about species composition and distribution of rusts. At the same time, data on their fossil remains are very scarce and scattered (Debey, Ettingshausen, 1857; Dilcher, 1965; Wolf, 1969; Tiffney, Barghoorn, 1974; Ramanujam, Ramachar, 1980). As a result, in recent publications (McTaggart et al., 2016; Aime et al., 2018), the time of origin of the Pucciniales and the divergence of its main clades is calibrated mainly by the age of the host plants and fossil remains of other groups of fungi. According to the latest data, rust fungi have separated from their closest relatives about 215–230 Ma ago, i.e., much later than the emergence of seed plants, but before the appearance of the early Pinaceae (Aime et al., 2018).

The spores in the studied amber sample undoubtedly belong to one of the representatives of the genus *Nyssopsora*. The teliospores of two other genera of rust fungi, *Triphragmium* Link and *Triphragmiopsis* Naumov, also consist of three cells, but their wall is warty and not covered with appendages.

The genus *Nyssopsora* was originally described in 1906 by D.Ch. Arthur (1906). During the 20th century, several monographic treatments of this taxon appeared (Lütjeharms, 1937; Monoson, 1974; Lohsomboon et al., 1990). In the last of these, nine species are listed for the genus and their teliospores are described as "borne singly on pedicels, composed of 3 cells, arranged as one basal cell attached with pedicels and two cells above, walls pigmented, bearing conspicuous projections, entire or branched at the tips" (Lohsomboon et al., 1990, p. 909). In 2014, one more species of this genus was added from Panama (Carvalho et al., 2014).

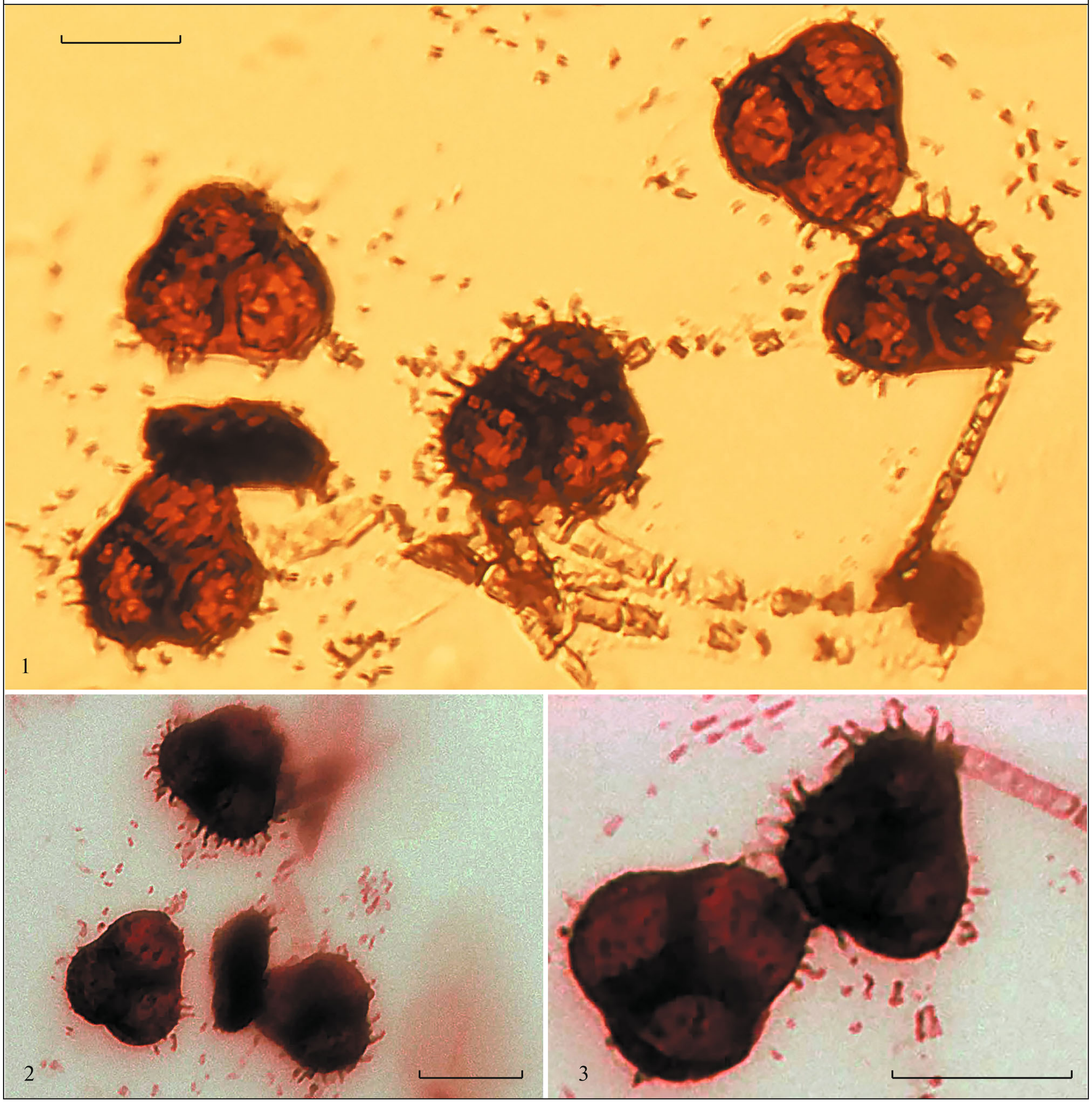
The spores we observed are very similar to the teliospores of the modern species *Nyssopsora trevesiae* (Gäum.) Tranzschel. Of all the *Nyssopsora* species known to date, only in *N. trevesiae* and *N. echinata* (Lév.) Arthur the teliospore appendages, as a rule, do not have branches at the apex, but in *N. echinata* they are much longer (up to 18 μm), and the teliospores themselves are much darker than those of *N. trevesiae*. The morphological characters of teliospores in the studied amber sample generally correspond to those in the description of *N. trevesiae*: "teliospores 3-celled, trigonal-subglobose or pyriform, not at all or slightly constricted at the septa, 24–37 × 25–36 μm (av. 31 × 29 μm); walls uniformly 0.5–2.5 μm (av. 1 μm), golden-brown to cinnamon-brown, with 10–23 spines in each spore, usually sharply pointed or rarely bifurcated at the tips, 2–9 μm long (av. 6 μm)" (Lohsomboon et al., 1990, p. 911). Of the differences, we can only point out that some appendages, although not branched, are hooked at the apex.

The function of the appendages on the surface of the teliospores of rust fungi remains not quite clear; presumably they do not aid buoyancy of spores in the air, but rather contribute to the inadvertent transfer of spores by entanglement in the bristles on the legs and body of insects (Savile, 1989). Given the small isolated group of spores, the insect that got trapped into the resin supposedly managed to free itself from entrapment, but left in the exudate some of the spores entangled in its bristles.

In the Far East of Russia, only one species of the genus *Nyssopsora* is currently known, *N. asiatica* Lütjeh., parazitizing species of the genus *Aralia* L., recorded in the southern Kuril Islands, south of Sakhalin and in the Primorsky Krai (Azbukina, 2005). The appendages on the wall of its teliospores are branched at the apex and thus are sharply distinguished from the spores of the fungus in the amber sample.

There are no noticeable plant inclusions in the examined amber sample. However, taking into account that rust fungi are obligate parasites of vascular plants and *Nyssopsora* species are rather narrowly specialized in infecting the particular host species of the Apiales and Sapindales orders, it is possible to make some

Plate 12



Explanation of Plate 12

Figs. 1–3. Teliospores of the rust fungus of the genus *Nyssopsora* in the sample of Sakhalinian amber PIN no. 3387/973. Scale bars 30 μm.

assumptions on the systematic position of the plant on which the investigated teliospores developed.

Current data on the hosts and geographical distribution of modern species of the genus *Nyssopsora* can be summarized as follows. On plants of the order Apiales, six species were recorded: *N. asiatica* (on Araliaceae in China, the Russian Far East and Japan), *N. citriobati* Syd. (on Pittosporaceae in Australia), *N. clavellosa* (Berk.) Arthur (on Araliaceae in Canada and USA), *N. echinata* (on Apiaceae in Europe and western North America), *N. thwaitesii* (Berk. et Broome) Syd. (on Araliaceae in China, India, Indonesia, Thailand, the Philippines and Sri Lanka) and *N. trevesiae* (on Araliaceae in China and Indonesia). On plants of the order Sapindales, four species have been reported: *N. cedrelae* (Hori) Tranzschel (on

Anacardiaceae, Meliaceae, and Simaroubaceae in India, China, Korea, Taiwan, and Japan), *N. formosana* (Sawada) Lütjeh. (on Sapindaceae in China, Taiwan and Japan), *N. koelreuteriae* (Syd. et P. Syd.) Tranzschel (on Sapindaceae in China and Japan) and *N. panamensis* A.A. Carvalho et E. Esquivel (on Anacardiaceae in Brazil and Panama).

The center of species diversity, and apparently of the origin, of the genus *Nyssopsora* is East Asia, where six species were reported. In North America and South Asia, two species have been recorded in each; in Europe, Australia and South America—only one species in each.

It should be also noted that the host plants of modern species of the genus *Nyssopsora* belong exceptionally to two phylogenetically distant orders, Sapindales and Apiales. The family Pittosporaceae, for a long time assigned to the Rosales, only relatively recently was finally placed within the Apiales (Plunkett et al., 1996; Chandler et al., 2007), although it was much earlier considered related to Apiales by the presence of secretory channels (Van Tieghem, 1884), a very stable feature of the higher Apiales that allows to recognize a plant in nature by scent. A species of *Nyssopsora* parazitizing plants of Pittosporaceae family provided an evidence of this since it was described in 1938 (Sydow, 1938). All known species on the Sapindales representatives develop uredinia and telia, while all parasites on Apiales belong to microcyclic species that form only telia. Based on this, V.G. Tranzschel (1925) suggested that microcyclic species evolved from full-cycle species with uredinia and telia on Sapindales and aecial stage on Araliaceae or Apiaceae, and that *N. cedrelae* and *N. koelreuteriae* may be heteroaecious and develop aecia on plants of the Araliaceae or Apiaceae. However, this has not yet been confirmed by observations in nature; moreover, it has been experimentally proven that *N. cedrelae* forms aecia of the Uredo-type, uredinia and telia on the same host plant, and therefore, is autoaecious (Kakishima et al., 1984). Both Apiales and Sapindales separated from their sister clades at the end of the Early Cretaceous (Nicolas, Plunkett, 2014) or in the Late Cretaceous (Patel et al., 2000; Muellner-Riehl et al., 2016), so the time frame for dating the origin of the genus *Nyssopsora* remains very broad.

The modern species *N. trevesiae* parasitizes plants of the Araliaceae: *Trevesia sundaica* Miq. in Indonesia (Lütjeharms, 1937; Lohsomboon et al., 1990) and *Brassaiopsis ciliata* Dunn (syn. *Euaraliopsis ciliata*) in Southern China (Zhuang, Wei, 2009). Therefore, it can be assumed that the plant on which the teliospores from the studied amber sample formed most likely belongs to the group *Trevesia* Vis.—*Brassaiopsis* Decne. & Planch. This in turn confirms paleofaunistic indications of rather warm and humid climate of the Sakhalinian amber forest (Baranov et al., 2015); extant species of the mentioned genera are characteristic of the undergrowth of humid subtropical and tropical forests stretching from the Himalayas through China, Thailand and Vietnam to Indonesia. According to molecular chronology, the group of genera *Trevesia*—*Brassaiopsis* exists as a separate clade of the Araliaceae from the early Eocene (Valcárcel et al., 2014), which is consistent with the age of the studied amber sample. The divergence of this group into the genera *Trevesia* and *Brassaiopsis* occurred in the Miocene about 20 Ma ago (Mitchell, Wen, 2005).

A summarizing monograph devoted to the Paleogene flora of South Sakhalin (Kodrul, 1999) does not contain any data on representatives of *Trevesia–Brassaiopsis* (as well as other species of the Araliaceae); however, in the section Plantae incertae sedis, leaf prints of "*Broussonetia*" cf. *kamtschatica* are provided for the Naibuchi and Snezhinka formations of the middle Eocene of Sakhalin. According to T.M. Kodrul, by a number of morphological characters, the samples differ from species of the genus *Broussonetia*, which does not allow their reliable attribution to this genus. By venation type, similar morphology of leaf blades and dentate leaf margin they are closer to the representatives of the Araliaceae. In our view, this description largely corresponds to the features characteristic to the modern *Trevesia-Brassaiopsis* group. Obviously, the taxonomic position of "*Broussonetia*", as it was argued by T.M. Kodrul, requires further study.

The oldest known fossil records of Araliaceae, reliably referred to this family, are of the early and middle Eocene age (Dillhoff et al., 2005; Martínez-Millán, 2010); the oldest reliable record at the genus level (middle Eocene) is the one of the extant genus *Dendropanax* Decne. et Planch. (Mitchell et al., 2012) known from East and Southeast Asia, Central and South America. Molecular phylochronology data indicate the middle Eocene as the time of diversification for the East Asian Araliaceae (Li, Wen, 2014), or the Eocene for most Aralian clades and the Eocene–Oligocene boundary for Asian Palmate clade (Nicolas and Plunkett, 2014). Our report presents a fossil evidence in favor of the first, more ancient dating, although undoubtedly further finds may increase the age of the Araliaceae.

ACKNOWLEDGMENTS

We consider it our pleasant duty to express our gratitude to A.P. Rasnitsyn and I.D. Sukacheva (PIN) for the possibility to study Sakhalin material, V.V. Martynov (Slavyansk) for detecting this inclusion during sorting the amber collection, A.P. Vlaskin (Institute of Zoology, NASU, Kyiv) for polishing the sample, A.A. Oskolsky (Botanical Museum, Komarov Botanical Institute, RAS, St. Petersburg) for valuable remarks and comments on the age of the Araliaceae, and N.P. Maslova (PIN) for constructive comments and suggestions.

FUNDING

The study was supported by the RFBR grant no. 19-04-00046 (DV).

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