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New fossils of ascomycetous anamorphic fungi from Baltic amber

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ABSTRACT

Three new fossils of saprotrophic fungi are presented and described from Baltic amber, dated to Eocene epoch (Paleogene, upper to mid-Eocene). All belong to Ascomycota and are represented by hyphae as well as asexual reproduction structures allowing to assign them to present genera, respectively *Periconia*, *Penicillium* and *Scopulariopsis*. These material provide both the first and the oldest known fossil record of the mentioned taxa, making these data valuable for the knowledge about the evolutionary history of the Ascomycota.

1. Introduction

The fossil records are crucial for better understanding of the evolution of currently living organisms. Fungi as soft-bodied, ephemeral microorganisms have low fossilization potential and are rare in the fossil record, except spores in palynological data, thus every single specimen is an important discovery providing new data (Briggs, 2003; Beimforde et al., 2014; Taylor et al., 2014). Amber, a fossilized tree resin is a remarkable source of remains of small animals, plants and fungi. One of the best known types of amber with largest deposits in the world, is Baltic amber, dated for upper Eocene epoch (Priabonian, 34–38 Ma) (Perkovsky et al., 2007; Sadowski et al., 2017). Inclusions in the resin are usually well preserved, allowing to uncover thousands of extinct organisms (Weitschat and Wichard, 2010). Currently more and more of unambiguous fossil fungi are described from all fossil resins, including Baltic amber (Dörfelt and Schmidt, 2005, 2007; Tuovila, 2012; Schmidt et al., 2013, 2014; Kettunen et al., 2015, 2018). Baltic amber, Dominican amber and recently, Burmese amber are the mostly cited as a source of fungal remains. The known fungal specimens represent various ecological groups (lichens, insect and plant pathogens, saprotrophs) belonging to the two main fungal lineages (Ascomycota, Basidiomycota) as well as a few from basal fungal lineages such as Mucoromycotina or Entomophthoromycotina. The strict taxonomic affinity of several specimens remains uncertain. However many specimens of dubious affinities were also found and described as new taxa (Beimforde et al., 2014; Taylor et al., 2014).

The phylum Ascomycota consists of over 64 thousand species. Many of them are widespread and common in nearly all habitats especially prevalent to plant litter, litter and different types of soil (Kirk et al., 2008). Most ascomycetes are pleomorphic with the anamorphic asexual form, being often more common than sexual and in this form, they are usually called hyphomycetes or molds. Anamorphs are often microscopic, hyaline or melanized and usually ephemeral. The high relative humidity permits and stimulates their growth. In some cases, proper identification of hyphomycetes, requires special treatment, staining of microscopic slides,

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observation of growth pattern on different types of media and careful analysis of the sporogenous structures (Ellis, 1976; Seifert et al., 2011).

The aims of this study were to find and to identify with the most possible accuracy fossils of anamorphic fungi associated with inclusions of organic matter, from Baltic amber.

2. Materials and methods

The pieces of amber with inclusions of organic remnants from European amber collections from museums of Warsaw, Gdańsk and selected specimens of Christel and Hans Werner Hoffeins amber collection, a repository of the Senckenberg Deutsches Entomologisches Institut Müncheberg were examined for the presence of fungal structures. Among all inclusions, only three were preserved well enough for the description of fungal structures. Data for fossil fungi specimens are summarized in the Table 1.

To avoid destruction of the numerous syninclusions in amber specimens, grinding and polishing were very carefully applied, using fine sandpaper. Preparation and photographic documentation of the inclusions were made at the Laboratory of Microscopy of the Department of Invertebrate Zoology and Parasitology, University of Gdańsk. Details were examined using transmitted and reflected light microscopy using a Nikon SMZ800 and Leica M205A stereoscopic microscope equipped with a Leica DFC 495 digital camera operating under the control of Leica Application Suite 3.7 program. The amber specimens no. MAIG 5947 and CCHH1677-7 were initially cut and grinded manually, already embedded in polyester resin, as described in Hoffeins (2001) and did not require additional processing. The third, MAIG 3586, was only pre-grinded and polished. The documented fungal structures were compared with the currently known anamorphic fungal forms, especially with those isolated from plant remnants and litter (Ellis, 1976; Ellis and Ellis, 1985; Seifert et al., 2011).

3. Results

As a result of the screening of amber collections, three fungal specimens were found and carefully analyzed. All of them represent asexual forms of reproduction and were assigned to Ascomycota. First one is highly melanized, while the second and third are hyaline. The size of the fungal structures in all cases does not exceed 500 μm. The first specimen produce spores in the acropetal chains, while the second and third one – basipetal.

3.1. *MAIG 5947 (CCHH92-5, donation to MAIG)*

Assigned taxon: *Periconia* sp.

3.1.1. *Description*

The amber unit no. MAIG 5947 consists of inclusions of unidentified epigeic Collembola (most likely from the order Entomobryomorpha, former order Arthropleona) and the fungal colony, which occurs on plant debris or on soil particle (Fig. 1A, B). As a fungal structure, we can distinguish an aerial hyphae, dark conidiophores with conidia in short acropetal chains (Fig. 1B–D). Aerial hyphae are septate, 100–250 μm long and 10–25 μm wide. Vegetative, substrate hyphae are sparse, unbranched and branched, usually 50–70 μm long, and 1–4 μm wide. Aerial mycelium consists of conidiophores and several sterile, non-branched setae. Conidiophores are macronematous, darkly pigmented, brown, blackish, arising solitary from the substrate mycelium; usually unbranched or branched singly in the upper part of conidiophore, 1–4 μm wide at the base. The length of the conidiophores ranges from 100 to 250 μm long. The apical part of conidiophores is slightly enlarged, and reaches up to 15 μm in diam. and is formed on the top of conidiophores (Fig. 1C, D). Conidia form a short, brownish-black acropetal chain. Based on microscopic observation conidiogenous cells seems to be globose, monoblastic or polyblastic usually 5–15 μm in diam.

The last conidia in chains are regularly globose, attached to sporogenous cell, 3–4 μm diam (Fig. 1D, marked with an arrow).

3.1.2. *Notes*

The morphological features described above are characteristic of the genus *Periconia* (Barnett, 1960; Domsch et al., 1993). Presented specimen of *Periconia* is relatively smaller than currently known members of this genus e.g. *Periconia byssoides* with conidiophores up to 350 μm or *Periconia pseudobyssoides* with conidiophores up to 1000 μm (Markovskaja and Kačergius, 2014). The type of conidiophore of described specimen with well-defined conidial heads is typical for genus and resembles *P. byssoides, Periconia psudobyssoides, Periconia cookei* or *P. alaeidis* illustrated by Hyde et al. (2018) and Seifert et al. (2011). Other *Periconia* species are much less similar to the described specimen due to lack of terminal heads or asymmetry in branching patterns. However, we refrain from describing a new species due to lack of sufficient difference from known species. The loose arrangement of sporogenous structures on the substratum and quite large, dark, macronematous conidiophores are typical for species of the genus *Periconia.*

The other extant fungi with similar morphology usually form synnematous structures. In the examined material the conidiophores are clearly build of single separate hyphae. It is a character which helps to distinguish *Periconia* from other melanized fungi belonging to genera *Graphium*, *Seifertia*, *Cephalotrichum*, *Cephalotrichiella* and others. The special attention should be paid to similar species occurring on contemporary resin – *Sorocybe resinaae* (Seifert et al., 2007). All aforementioned species could be, however, clearly distinguished from the presented fungus by complex conidial stalks. Moreover, most of them, except from *Sorocybe,* produce small, lightly colored spores (Partridge et al., 2002; Crous et al., 2014; Li et al., 2016; Sandoval-Denis et al., 2016). The brown, single hyphal stalk is formed by some members of anamorphic Ascomycota: among others *Leptographium*, *Grosmannia*, *Graphiopsis* (syn. *Dichocladosporium*), *Thysanophora, Haplographium.* Presented *Periconia*-like specimen differs from all aforementioned genera by quite large, spherical spores (Fig. 1C, D). The differences in color could represent taxonomically important features (melanization of mycelium is thought to represent a defense against UV radiation) as well as result of taphonomic

Table 1
Summary of detected inclusions with fungal structures (specimen ID, amber collection name and taxon assignment).

No.	Collection	Number of amber specimen	Assigned genus:
1.	Repository of Museum of Amber Inclusions, University of Gdansk (MBI)	MAIG 5947 (CCHH 92-5)	*Periconia* sp.
2.	Repository of Museum of Amber Inclusions, University of Gdansk (MBI)	MAIG 3586	cf. *Penicillium* sp.
3.	Repository of Senckenberg Deutsches Entomologisches Institut Müncheberg, Christel and Hans Werner Hoffeins amber collection.	CCHH1677-7	cf. *Scopulariopsis* sp.

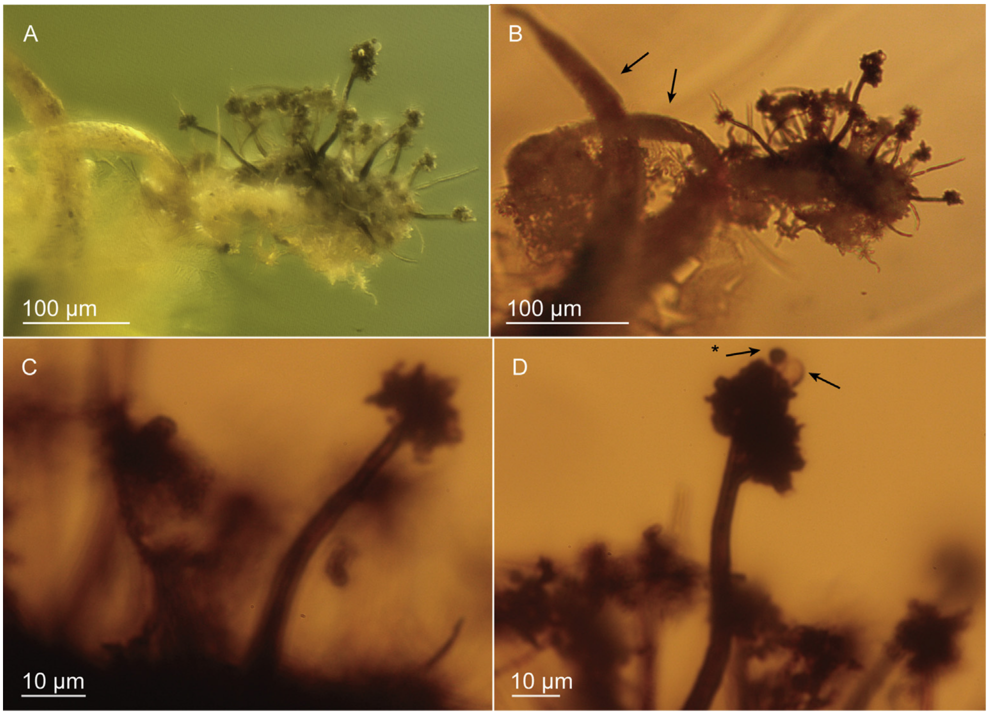

Fig. 1. MAIG 5947 (CCHH92-5). (A) Light microscopy of colony morphology. General view of a colony of *Periconia* conidiophores, (A) in incident light; and (B) in transmitted light. (B) Furcula of the Collembola next to the colony marked with arrows. (C) Single unbranched conidiophore with cell walls. (D) The largest conidiophore with branching base, bearing spores (marked with an arrow and asterisk).

processes. We are convinced that the color of conidiophores is an immanent feature of the fungus. All parts of the fungal colony are colored homogeneously and are well preserved, same as other parts of inclusion.

The genus *Periconia* Tode 1791 with *Periconia lichenoides* Tode as a type species, is relatively large and recently certain species from other closely related genera have been transferred to this genus (Seifert et al., 2011; Tanaka et al., 2015), resulting in more than 180 species of *Periconia* recorded currently in MycoBank (2017) and 199 species and varieties in Index Fungorum (2016). However, the genus *Periconia* and its relatives are separated from the Massarinaceae by Tanaka et al., (2015) and placed in a resurrected family, the Periconiaceae. *Periconia* usually occurs on detritus but is also noted as pathogen or endophyte of living plants (Markovskaja and Kačergius, 2014). This cosmopolitan genus, reaches about 40 species occurring on leaves, wood, bark and litter of many plants (Romero, 1994; Photita et al., 2001; Yanna et al. .2002). It is also isolated from freshwater and marine habitats (Cai et al., 2002; Morrison-Gardiner, 2002) as well as from mangrove forest areas (Alias and Jones, 2000; Sarma and Vittal, 2000). *Periconia* sp. was also noted as endophyte and pathogen of *Parthenium* (Asteraceae) (Romero et al., 2001).

Fungi of the genus *Periconia* usually produce macronematous conidiophores with short branches only in the upper part, where spores are formed, in short, sometimes branched chains, or more rarely micronematous conidiophores branching in irregular manner e.g. *Periconia variicolor* (Cantrell et al., 2007).

The spores are large, spherical (Fig. 1C, D). The only feature well demonstrated by this specimen is the dimension and shape of spore. The wall ornamentation, which should be important for species identification, unfortunately is not possible to observe in the presented specimen.

The fungal inclusion forms well-defined conidial heads. The most similar fossil fungus from amber is *Gonatobotryum piceae*. It is also dated for Eocene epoch and occurs on the remnants of hypocotyls of *Picea baltica* (Dörfelt and Schmidt, 2007). The main difference between *G. piceae* and fungus presented here is a shape of conidiophore with conidia, which are arranged partly coronary as well as the pattern of sporulation.

3.2. MAIG 3586

Assigned taxon: cf. *Penicillium* sp.

3.2.1. Description

Amber specimen no. MAIG 3586 contains numerous inclusions such as Diptera (Sciaridae), Hymenoptera (Formicidae) and unrecognizable insects, which are partially or fully covered with milky impurities (Mierzejewski, 1978) with fragile filamentous structures. The matrix amber also contains plant remnants, soil particles with numerous unidentified organic structures as well as the presented fossil fungus. The fungal colony is a hyaline sporogenous asexual state and is growing directly on the surface of putative plant remnants (Fig. 2A, B). It forms a few, approximately six clusters containing from 3 to 7 conidiophores each (Fig. 2B–D). Conidiophores are monoverticillate (occur with phialides arising directly from the top of conidiophore), some of them may be distinguished as biverticillate (Fig. 2B–D). A vegetative, substrate hyphae are sparse, both unbranched and branched in clusters, usually 100–500 µm long, and 50–100 µm wide (Fig. 2A). The average size of conidiophore, with globose brush-shaped heads, is 100 µm and with conidial chains usually 30–40 µm long and 15–40 µm wide (Fig. 2D, marked with an arrow). Brush-shaped conidiophores consist of secondary branched metulae and phialides with chains of globose spores. Conidia are formed in basipetal chains, attached to phialides and conidial heads. The size of isolated spores in the amber matrix is between 2 and 8 µm (Fig. 2D, marked with an arrow).

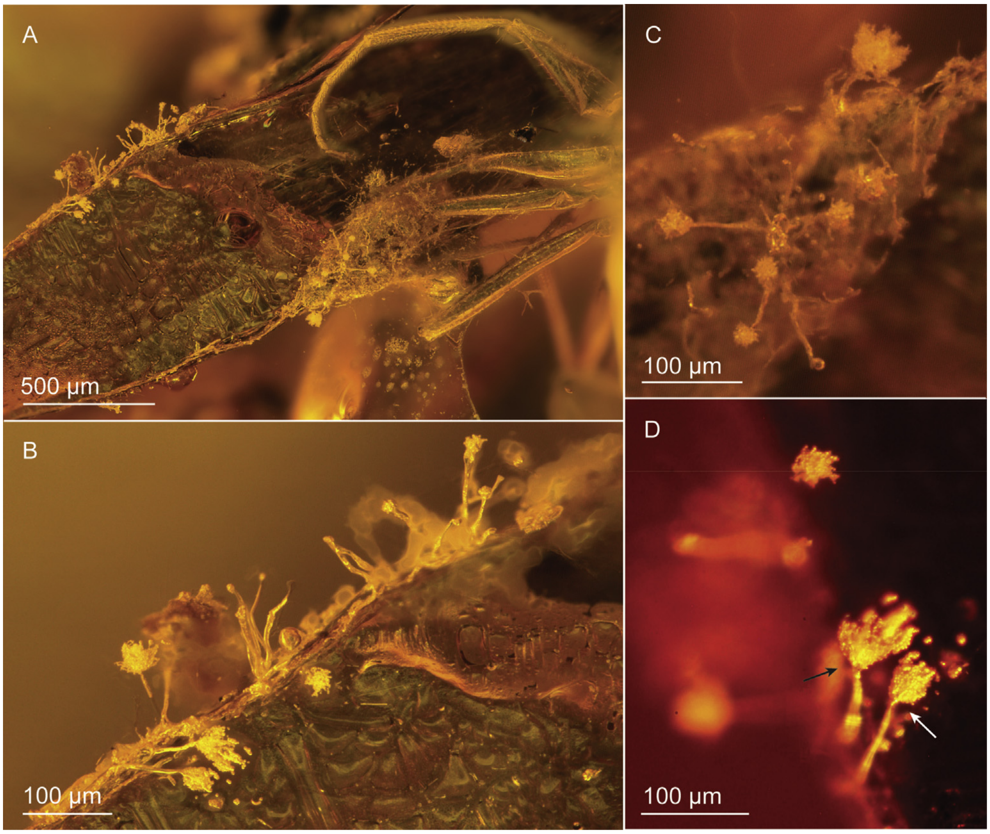

Fig. 2. MAIG 3586. (A–C) General overview of colonies of *Penicillium* on the surface of plant fragment. (B–D) Brush-like conidiophores with isolated spores. (D) Phialides arising directly from the top of conidiophore (marked with an arrows).

3.2.2. Notes

Brush-shaped conidiophores of specimen no. MAIG 3586, are similar to conidiophores of recent genus *Penicillium* (family Trichocomaceae) (Barnett, 1960; Domsch et al., 1993). Proper identification of species is often possible only observing growth pattern and using molecular methods. The presence of two branching levels visible on some conidiophores (metulae and phialides level) is the strong support for *Penicillium* affinity of the fungus. The modern genus *Penicillium* includes more than 350 species with many synonyms (Samson, 2002; Visagie et al., 2014). Some species of *Penicillium* (from former monoverticillata section) would be similar to *Aspergillus* species, but generally, they do not have branching conidiophores.

The conidiophores of several, currently living ascomycetous families could be morphologically similar to the described specimen, but some features allow us to recognize it as *Penicillium*. The similar brush-like conidiophores are formed by *Geosmithia* (Nectriaceae, Hypocreales) but cylindrical conidia produced by this fungus exclude such assignment. Another similar genus is *Thysanophora*. However, it differs in having melanized, sympodially branched, and usually much more robust conidiophore (Visagie et al., 2014; Seifert et al., 2011). In this amber specimen, we can distinguish easily the separate chains of spores. The other fungi with regularly branched apical part of conidiophores are *Paecilomyces* (Trichocomaceae, Eurotiales) and *Isaria* (Clavicipitaceae, Hypocreales). The above-mentioned genera have more irregularly branched conidiophores, often form synnemata and are typically insect pathogens. The general characteristics, as well as frequent occupancy of similar ecological niches by currently known *Penicillium* species and worldwide distribution of *Penicillium*, make it undoubtedly the most likely taxa (Domsch et al., 1993).

Observed differences, among shape and size of brush-like heads of conidiophores, may suggest the different life stage like immature reproductive structures, with some ripe, isolated conidia in the amber matrix or dried, deformed due to taphonomic processes. It is also highly probable that in MAIG 3586 amber specimen, syninclusions showed on Fig. 2A, B with the cluster of six conidiophores, may belong to different taxon of Trichocomaceae. Conidiophores of this cluster are similar to conidiophores of *Aspergillus collembolorum*, with apical enlargement of conidiophore and dense, radial chains of small spores (Dörfelt and Schmidt, 2005). The potential cause of such differences in size of spores may be connected with air vesicles which arose on the surface of spores during fossilization processes.

3.3. CCHH1677-7

Assigned taxon: cf. *Scopulariopsis* sp.

3.3.1. Description

The fungal colony consists of hyaline, numerous filamentous structures on dried and unidentified insect larva (most likely Coleoptera), with no other syninclusions or isolated fungal structures in the amber matrix (Fig. 3A, B). The total size of the larva with fungus is approximately 2500 μm. Vegetative mycelium is thin, slight bright with the average length in matrix amber 500–2000 μm, and width from 3 to 7 μm. Simple robust, micronematic conidiophores arise quite regularly from hyphae extending above the substrate. The broad apex of conidiogenus structure, without a neck is well visible on the Fig. 3C. Conidia are oval, with no visible ornamentation, 1–5 μm wide, located at the apex of hyphae in chains, usually with 3–12 spores (Fig. 3C).

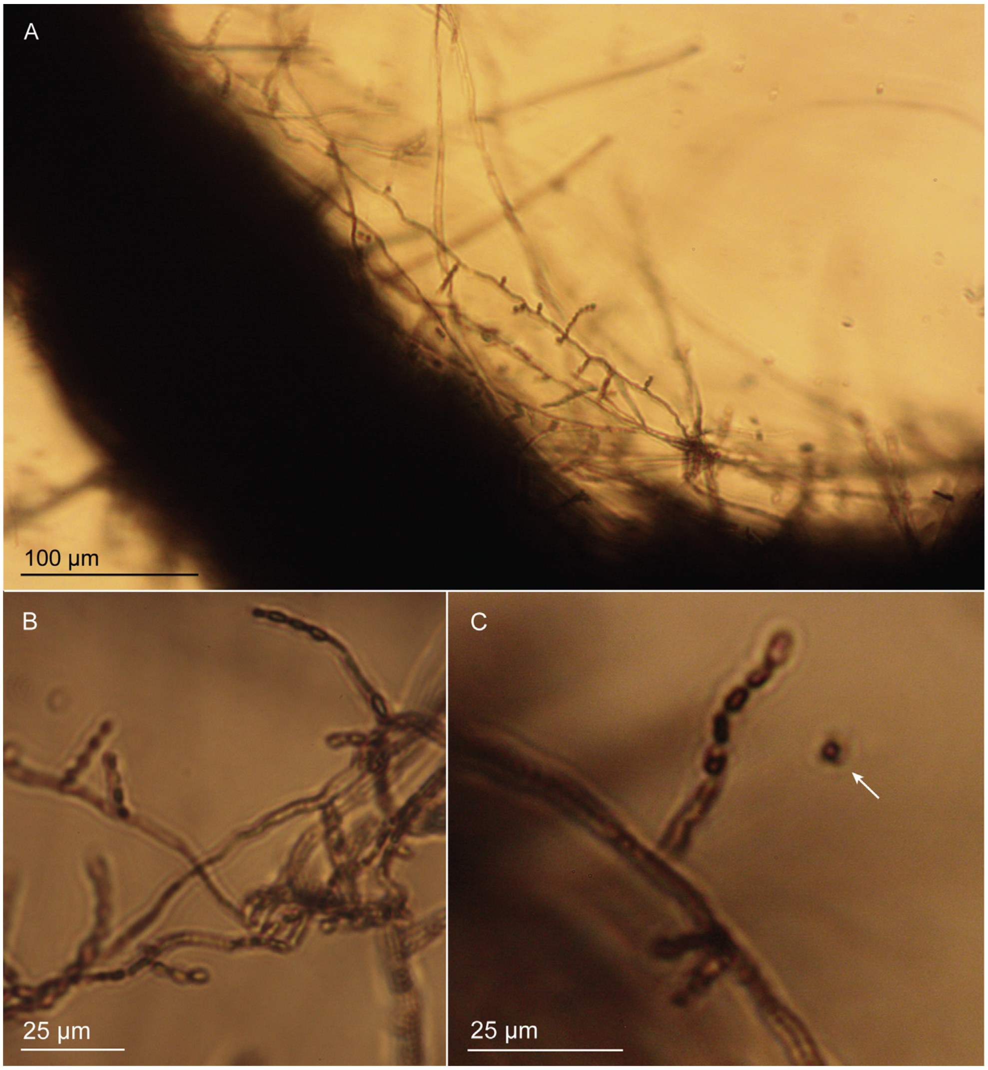

Fig. 3. CCHH1677-7. (A) Transmitted light of colony of *Scopulariopsis* like fungus on insect larvae. (B) Chains of spoeres with branching hyphae. (C) A chain of oval spores with one isolated in the amber matrix (marked with an arrow).

3.3.2. Notes

Features of inclusion no. CCHH1677-7 exhibit high similarity with species of the modern genus *Scopulariopsis*, which is represented by hyaline or brownish anamorphic fungi, saprotrophic or pathogenic to animals, especially arthropods (Samson et al., 2002; Yoder et al., 2003). *Scopulariopsis* species are common in soil, growing on plant and animal remains. The average size of described specimen is very close to the size of some *Scopulariopsis* species. A single chain consists of 9–12 spores and measures about 100 μm. The robustness of conidiophores and broad apex of conidiogenous structure suggests rather annelidic than phialidic origin of spores. Sandoval-Denis et al. (2016) redefined *Microascus, Scopulariopsis* and allied genera. The authors based on the Genealogical Phylogenetic Species Recognition (GCPSR) criterion decided to change the affinity for some *Scopulariopsis* strains and placed them in *Microascus*. We believe that presented specimen belongs to *Microascaceae* family, however we decided to use the name *Scopulariopsis* because of the same type of asexual reproduction. The name *Microascus* which is traditionally used for teleomorphic form of reproduction could be misleading in this case. The certain affiliation to the genus *Scopulariopsis* or closely related anamorphic *Microascus* cannot be determined without genetic analysis. However only some of *Scopulariopsis* and *Microascus* anamorphs produce hyaline spores. The most similar to presented specimen are *S. albida* isolated from soil, *S. africana* obtained from mud and salt pan (Wundenberg et al., 2017) and *M. expansus* isolated from clinical samples (Sandoval-Denis et al., 2016).

Similar genera *Monilinia* or *Phialosimplex* can be excluded because they are pathogens of either plants (Vasić et al., 2016) or mammals (Sigler et al., 2010). There also some morphological similarities with sooty molds, occurring on the surface of leaves, which are however usually dark pigmented (Rikkinen et al., 2003; Kettunen, 2016). It is not fully possible to exclude genus *Penicillium* or other genera of Trichocomataceae family. Some of its representatives may form conidiophores with solitary phialides, but usually, they are much smaller and slender than in presented specimen and tend to have a neck (Visagie et al., 2014). Hyaline and bright conidia forming chains are also characteristic for the modern genus *Cladophialophora*, which is a human pathogen, uncommon in soil with longer and more cylindrical spores in long, sometimes branched chains (Badali et al., 2008). Some species of *Aspergillus* subgenus *Polypaecilum* also show high similarity to presented fossil but usually, they have no chains of conidia and spores are single, attached to elongated hypha (Tanney et al., 2017). We also reject the genera *Simplicillium, Lecanicillium, Verticillium* and relative genera as a possible fungus affiliation.

4. Discussion

Several specimens of ascomycetous fungi are known from Baltic amber. Most of them are represented by unidentified anamorphic stages without any features allowing correct identification or description (Kettunen et al., 2018). Lichens are possibly the best studied fossil fungi with 167 fossil specimens (Kaasalainen et al., 2017). Sooty molds were also repeatedly noted from amber and other fossil materials (Rikkinen et al., 2003; Schmidt et al., 2014; Kettunen et al., 2015, 2016). The representatives of ascomycetous fungi on arthropods – *A. collembolorum* on Collembola (Entomobryomorpha) (Dörfelt and Schmidt, 2005) and *Stigmatomyces succini* on imago of Diopsidae (Diptera) (Rossi et al., 2005).

Due to fossilization processes, taphonomic modification, optical transformations, and distortion by polymerized resin, all inclusions lost their genuine shape and size (Weitschat and Wichard, 2002), so caution is advised in using size and shape as diagnostic features. In our studied samples, conidiophores are surrounded by air vesicles or are shrink which makes it hard to distinguish single spores. In other cases, a high density of amber matrix may impact the visibility of single spores, as in *Penicillium* like species (Fig. 2D).

The presence of plant detritus and arthropods belonging to Collembola or Coleoptera, which may occur in humid and epigeic habitats, indicates that presented specimens inhabit soil litter of the Fennoscandian forest. Due to diverse ecological niches of the extant Ascomycota fungi, it is impossible to reconstruct climate condition based only on the presented fossils. However, it has been proposed that climate in the Eocene Fennoscandia was warm-temperate, rather than subtropical as previously thought (Słodkowska and Krasiński, 2016; Sadowski et al., 2017). All of these fossil fungi from recent genera could be ubiquitous, widely distributed in the world in all climate zones with exception of the polar regions (Domsch et al., 1993; Seifert, 2011), which develop on decaying organic matter, leaves, wood and rotting stems of plants or on animal remnants.

5. Conclusions

In this paper, we present fossils of saprotrophic, anamorphic fungi from Baltic amber on the organic, plant and insect remnants and describe their asexual life forms.

Due to the lack of precise information such as a growth pattern, sporulation type and proper size of most of the observed structures the correct taxonomic description is difficult. Therefore we decide to circumscribe them as much as possible, assigning with recent similar taxa, but we refrain from describing new species.

Presented fossil fungal taxa broaden the current knowledge about saprotrophic fungi in the history of the Earth and can be used as evidence of the existence of these three genera and families in the Eocene epoch as well as the lowest calibration point in molecular phylogenetic analyses.

Conflicts of interest

The authors declare that they have no conflict of interest.

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