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The biological inclusions in Eocene amber from Študlov locality in White Carpathian Mts.

Biologické inkluze zachované v eocénním jantaru z lokality Študlov v Bílých Karpatech

DIPLOMA THESIS

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I declare that the present thesis has not been submitted for the purpose of obtaining of the same or another academic degree earlier or at another institution. My involvement in the research presented in this thesis is expressed through the authorship order of the included publications and manuscripts. All literature sources I used when writing this thesis have been properly cited.

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Acknowledgements:

Abstract

The Študlov amber has been the only known fossil resin from the Czech Republic, in which the biological inclusions are preserved, and at the same time the only Czech fossil resin occurring not in the area of the Bohemian Massif, but in outer arch of the Outer Western Carpathians. So far, only single findings of fossil Hymenoptera and Diptera have been published. In contrast to mostly Cretaceous ambers of the Bohemian Massif, the age of Študlov amber is usually estimated from the late Paleocene to mid Eocene. This diploma thesis provides an overview of the fossil organisms found in the Študlov amber in the past two decades and it is also the most comprehensive text dedicated to the palaeodiversity of embedded organisms from this remarkable fossil resin. The presence of various microscopic fungi is proven, as well as the presence of angiosperm trichomes, mites and insects (prevailed by Hymenoptera and Diptera). The discovery of a hymenopteran family Stigmaphronidae (Apocrita) is the first Cenozoic evidence of this family, formerly considered as extinct by the end of Cretaceous. Finding of an isolated gymnosperm twig with wood anatomical characters close to genus *Glyptostrobus* allows to outline some conclusions about the paleoecosystem. The Eocene age of the resin is confirmed by the combination of biological and chronostratigraphical approaches.

Key words: Amber, fossil resin, fossil organisms, paleobiology, Eocene

Abstrakt

Študlovský jantar je jedinou fosilní pryskyřicí z území České republiky, v níž jsou nalézány biologické inkluze, a současně jedinou českou fosilní pryskyřicí nacházející se nikoliv na území Českého masivu, ale ve vnějším oblouku Západních Karpat. Dosud však byly publikovány pouze jednotlivé nálezy fosilních blanokřídlých a dvoukřídlých z tohoto naleziště. Na rozdíl od převážně křídových pryskyřic Českého masivu se stáří študlovského jantaru pohybuje v rozmezí svrchního paleocénu až středního eocénu. Tato diplomová práce poskytuje přehled fosilních organismů nalézaných ve Študlovském jantaru v minulých dvou desetiletích a je dosud nejrozsáhlejším textem pojednávajícím o biodiverzitě organismů v této pozoruhodné fosilní pryskyřici. Potvrzena je přítomnost četných mikroskopických hub, trichomů krytosemenných rostlin, roztočů a zejména dvoukřídlého a blanokřídlého hmyzu. Výskyt štíhlopasého blanokřídlého hmyzu z čeledi Stigmaphronidae je prvním doloženým eocénním příkladem persistence této skupiny, dříve uváděné jako vyhynulé na konci křídy. Nález fragmentu dřevnatého stonku, jehož dřevní anatomie je blízká rodu *Glyptostrobus* (cypřišovité, Cupressaceae), dovoluje učinit několik závěrů ohledně paleoekosystému. Díky kombinaci biologického a chronostratigrafického přístupu je potvrzeno eocénní stáří pryskyřice.

Klíčová slova: Jantar, fosilní pryskyřice, fosilní organismy, paleobiologie, eocén

CONTENTS:

1. Introduction

Resins of certain vascular plants can alter their chemical composition in the course of hundreds, thousands or millions of years. The resin, once meant to protect the plant from herbivores and pathogenes, changes into unique medium, which now helps us to discover the ancient world in remarkable structural detail. In case that the resin has not been fully matured, which means the polymerization and other chemical prosesses did not reach their maximum, it is called copal. The fully fossilised resin is called amber. At least 1 million years is necessary for the resin to become amber (Santiago-Blay & Lambert 2007). The degree of maturation can be determined thanks to Fourier transform-Raman spectroscopy (Brody et al. 2001). However, all begins with fresh resin. There are tree families with certain genera those were responsible for origin of most of amber deposits. Dipterocarpaceae and Fabaceae (genus *Hymenaea*) represent amber-producing angiosperms, while Pinaceae, Sciadopityaceae, Araucariaceae or Cheirolepidaceae are the well-known amber-producing gymnosperms. It is rather common that when there is an amber deposit, many aspects need to be considered: the stratigraphic position, chemical composition which can help to identify the plant producer, and especially the biological inclusions. The overall approach then gives us an ideal chance to extend our knowledge about life on Earth and its evolution.

In combination with appropriate properties of deposition site, resin offers spectacular conditions for conservation of organisms or their body structures. This has been documented since the upper Triassic (Roghi et al. 2006), though even 320 million years old Carboniferous (Palaeozoic) amber has been found, but so far containing no biological inclusions (Bray & Anderson 2009). In the history of humankind, amber was often highly appreciated mostly for its appearance or scent when ignited, and represented an important part of prehistoric fair. Majority of the fossil inclusions have been known from the Cretaceous, Paleogene and Neogene periods. Amber deposits can be found in dozens of localities (Penney 2010) (see below). Hovever, amber found in different deposits varies in quality, quantity and the amount of contained inclusions. It is almost sure that we still have not discovered all deposits of the fossil resin and thus we still can expect a number of crucial palaeobiological discoveries.

Amber fossils serve well at the moment when the macrofossils (bones or their parts, teeth, mineralised plants), and compression fossils do not provide us the kind of data we would like to gain. Sometimes the resin has such an exceptional preservation, that it reveals the bioinclusions not only in their 3D shape, but also very detailed, even up to the nanometers, often with the finest details captured, for example spider thread (Saint Martin et al 2014), fungal hyphae (Speranza et al 2015), plant chloroplasts (Koller et al 2005), or spirochete-like bacteria (Poinar 2015). Not always we do find only small-scale fossils. There are some significant inclusions recently found, which even caught attention of world massmedia; namely the earliest appearance of rainforest frog preserved in amber (Xing et al 2018), "A mid Cretaceous embryonic-to-neonate snake" (Xing et al 2018), "A mid Cretaceous enantiornithine (Aves) hatchling with unusual plumage" (Xing et al 2017) or "A Feathered Dinosaur Tail with Primitive Plumage Trapped in mid Cretaceous Amber" (Xing et al 2016), all of them from mid Cretaceous Myanmar amber.

Thanks to technological development, our possibilities of studying amber fossils have been greatly expanding during last years. In spite of the newest methods we will probably never be able to isolate DNA from bioinclusions (Roselló 2013). On the other hand, there are techniques as the computed microtomography which bring remarkable outcomes, giving us the advantage to recognize the contents of opaque amber samples and also the possibility to create 3D models of inclusions as well as virtual cuts of their parts (e.g., Soriano et al 2010, Perreau & Tafforeau 2011).

But mistakes do not avoid this branch of research. There is a considerable problem of easy confusion of plant, fungal or unicellular organism inclusions with inorganic material, artifacts of resin production and often also different species. In some cases re-determination of samples occurs (Kaasalainen et al 2015). We have to be careful mostly in case of unicellular organisms, because there is a relatively high probability of misinterpretation of tiny unknown inclusions as biological material instead of inorganic pseudoinclusions (Thiel et al 2016). Still majority of scientific community targets at larger inclusions with macrofossils, seeking for ancient diversity of arthropods or trying to better understand tetrapod palaeobiology and evolutionary history of recent groups.

1. 1. – World's most significant amber deposits

Before focusing on Študlov amber, a brief overwiew of world's most important amber deposits will be provided here. Only the most significant deposits can be mentioned, despite much more of them worth the interest. Martínez-Delclòs et al. (2004) introduced a list of over 160 worldwide localities of amber occurrence, not even including all of those which are known to us today. A complex overview of world's most important amber deposits, including their scientific importance, can be found in Penney (2010). At most of the localities, the amber lies in its original stratigraphic position (primary deposits), but somtimes it is redeposited by geological processes and separated from its former placement (secondary deposits). Not all the fosil resins do contain biological inclusions or have enough qualities to be studied. There is probably much more fossil resin hidden below the Earth's surface. Newly found deposits are being discovered by coincidence, for example during mining activities. Ambers have been found on all continents except Antarctica.

Fig 1. – Excerpt of ICS, International Chronostratigraphic Chart, focused on the Cretaceous period with position of major amber deposits; modified after Cohen et al. (2013; updated).
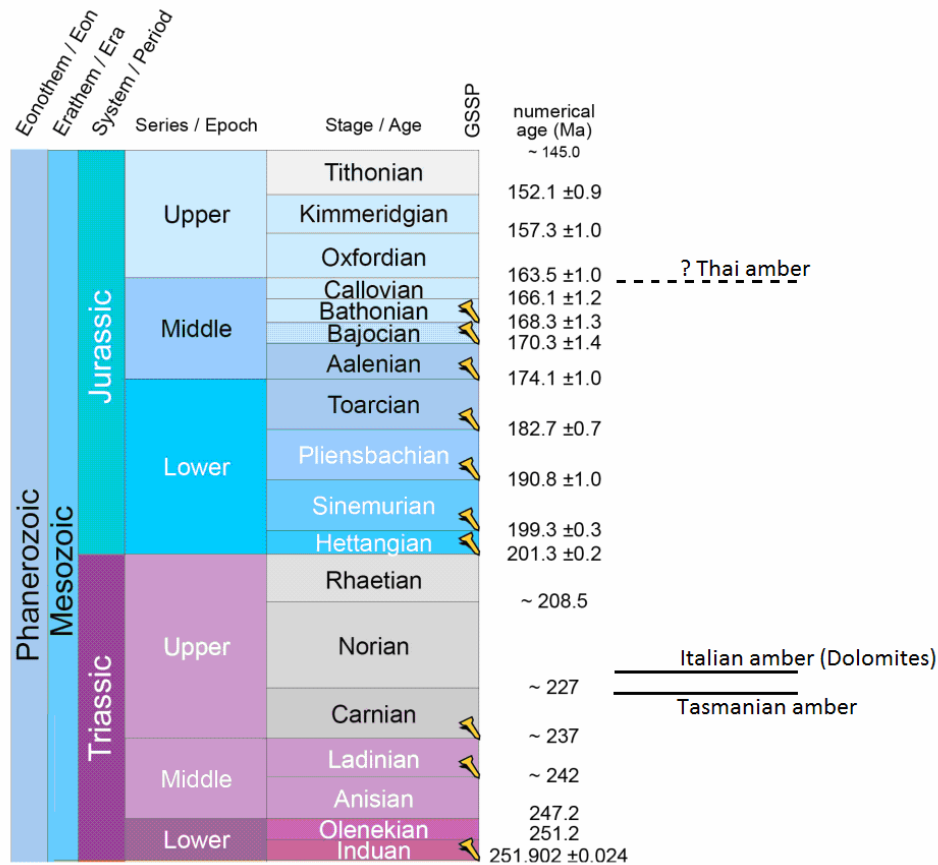
Fig 2. – Excerpt of ICS, International Chronostratigraphic Chart, focused on the Triassic and Jurassic periods with position of major amber deposits; modified after Cohen et al. (2013; updated).

1. 1. 1. – Mesozoic amber

(Figs. 1.; 2.)

Even before the Mesozoic era, plants were able to produce resin, which during ages became amber. The oldest known amber comes from the Carboniferous coal seam in Illinios, USA, originating in humid climate 320 Ma, and investigated in the sense of its chemical composition by Bray & Anderson (2009). However there is no evidence of fossil life.

After a long gap caused by Permian climate change, next evidence of amber production comes from the Triassic of Italian Dolomites – amber 220 million years old with its plant producer supposedly from Cheirolepidaceae family (Roghi et al. 2006). Schmidt et al. (2006) described a few microorganisms found in this amber, such as

microscopic fungal hyphae, bacteria or ciliates along with arthropods. Further Triassic amber can be found in Tasmania (Stilwell et al. 2020). Considered as ca. 230 million years old and described this year, it can not remain unnamed here, despite it only seem to contain inclusions such as tree bark remains.

Also Jurrasic amber is kind of rare. There is a deposit in Thailand, where a few-centimeter-sized amber pieces emerge (Philippe et al. 2005), or Italian Lower Jurassic deposit with amber containing minute plant inclusions (Neri et al. 2017). There are several deposits in Lebanon, where the Jurassic and also various Cretaceous ambers can be found (Penney 2010). The Cretaceous amber provides rich fauna and flora, while the Jurassic amber of Lebanon contains at most fungal inclusions (Azar et al. 2010). The Lower Cretaceous amber found in Lebanon represents a remarkable source of data. Several species of scale insects were described by Koteja & Azar (2008), from this amber which is ca. 130 million years old or slightly younger, probably Barremian (Maksoud et al. 2017). The most studied to date is the Burmese amber (Myanmar) with its immense spectrum of organisms trapped inside, still refining our understanding of evolution of life. The age is mid Cretaceous, Cenomanian, ca. 98 million years (Shi et al. 2012). Cockerell (1970) noticed the exceptional diversity of arthropods, but the interest in amber from Myanmar has not fallen since then. Here's only an example of lastest discoveries: a mole cricket *Tresdigitus* (Xu et al. 2020), rare holometabolan larva with piercing mouth cone (Haug et al. 2019), a piece of bird wing (Xing et al. 2020) or even various gastopod shells (Bullis et al. 2020). Apart from Burmese amber, a few other notable Cretaceous deposits should be mentioned here. At first the Albian Spanish amber, even older than the Burmese amber, with inclusions of fungal hyphae, isopods, mites, insects or arachnids (Delclos et al. 2007). Then there is the Albian/Cenomanian amber from Charentes in France, containing fossil microorganisms, plant remains, many arthropod inclusions and also vertebrate remains (Adl et al. 2011). But there are also Upper Cretaceous ambers worth of our attention such as the Turonian New Jersey amber, from which we mostly know the various hymemopterans, e. g. mymarromatid wasp described by Engel & Grimaldi (2007) or formicine ant described by Grimaldi & Agosti (2000). Last but not least there is a deposit of Campanian amber found in western Canada with some interesting hymenopterans (McKellar & Engel 2012), so one does not necessarily have to focus their Cretaceous amber research to the Cenomanian.
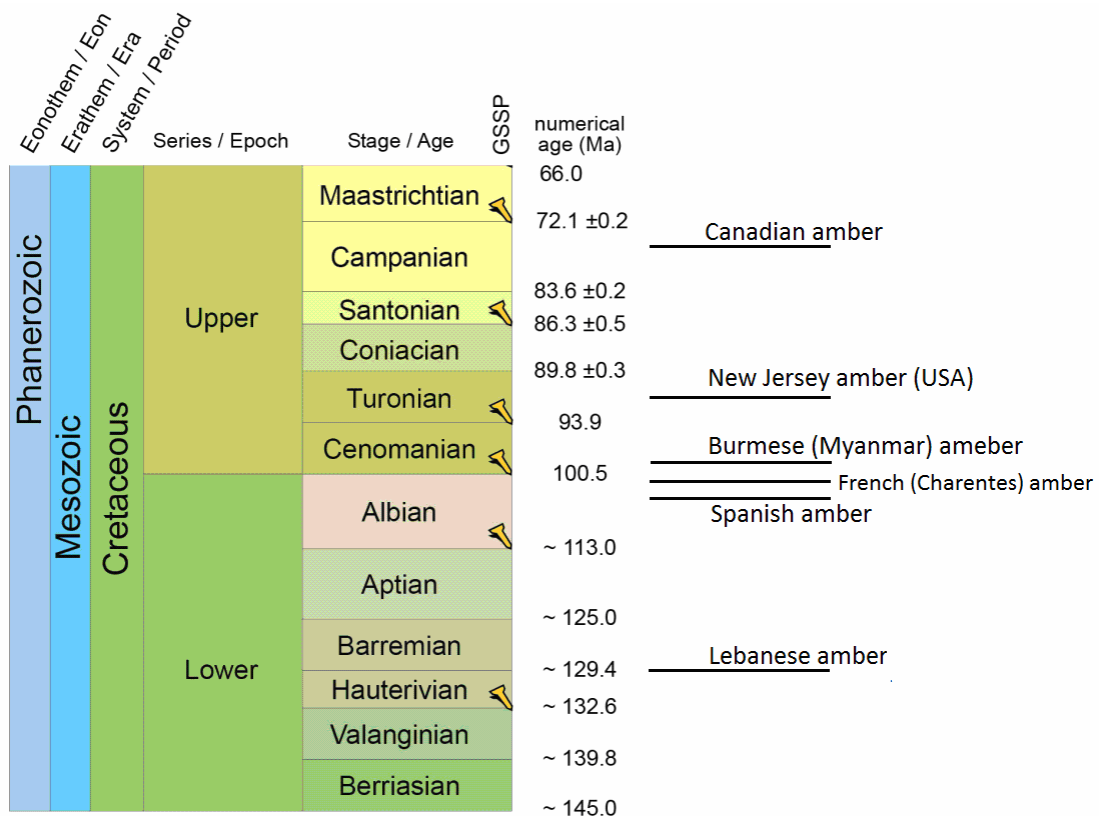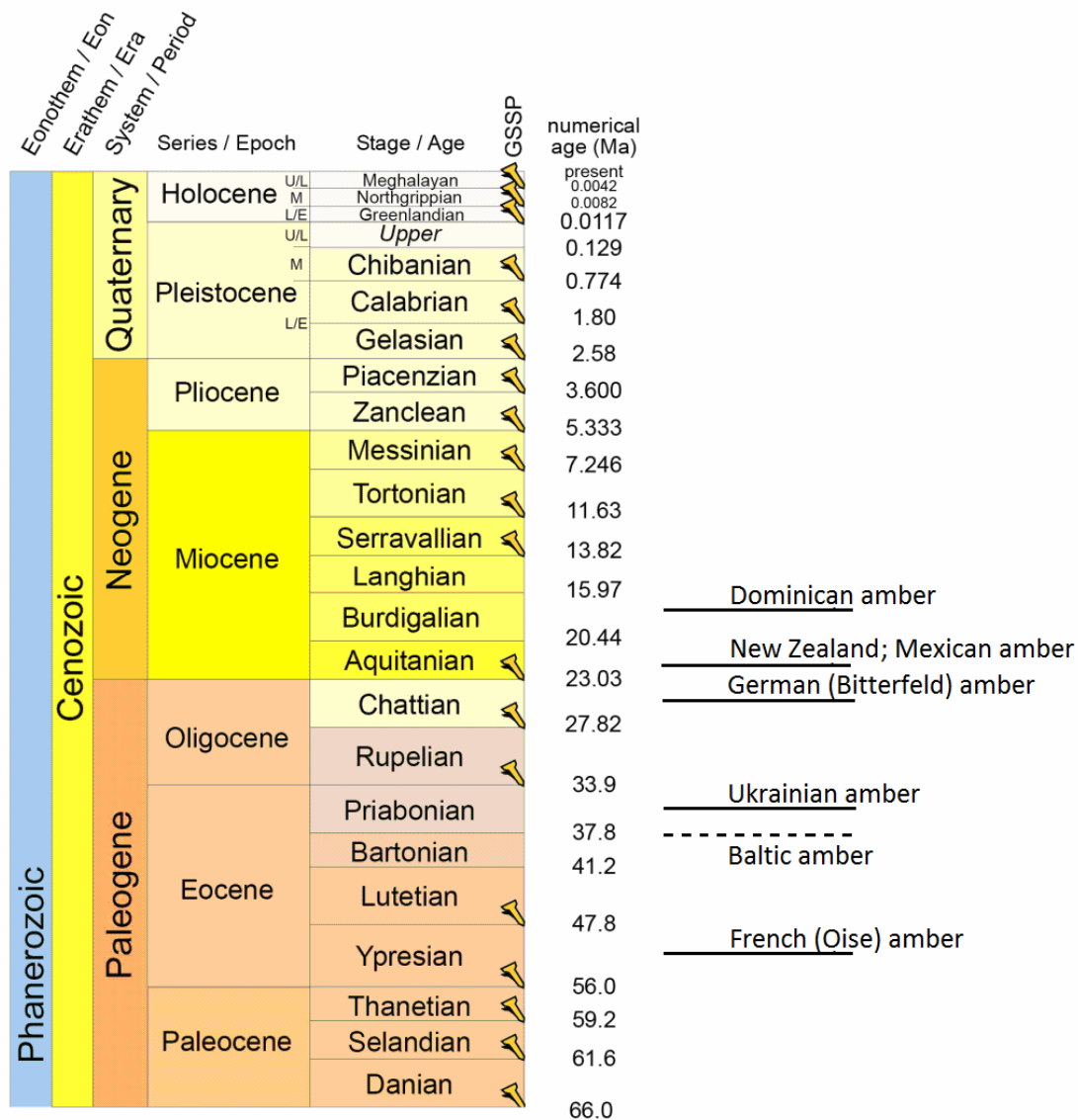
Fig. 3. – Excerpt of ICS, International Chronostratigraphic Chart, focused on the Cenozoic era with position of major amber deposits; modified after Cohen et al. (2013; updated).

## 1. 1. 2. – Cenozoic amber

(Fig. 3.)

Although there is some evidence of life from the Paleocene amber of Jamaica (Iturralde-Vinent 2001) the real boom begins in Eocene.

Baltic amber, known to human for millennia as matter of trade, has also been studied for the longest time. A huge amount of papers revealing the diversity o Baltic amber organisms has been published since 1900. Cockerell (1909) with his fine descriptions of

Hymenoptera or Brues (1923), describing new species o fossil phorid flies, were among the first researchers to pay attention to the Baltic amber inclusions. The enigmatic plant procucer of amber has been discussed recently. Wolfe et al. (2009) suggested it was a conifer from Sciadopityaceae family, Sadowski et al. (2017) analysed coniferous remains to show the diversity of coniferous trees that grew in the original forest, including Taxodiaceae, Pinaceae or Sciadopityaceae, and estimated the age of amber to the late Eocene. The investigation of Baltic amber lasts still, using modern techniques of observation and 3D reconstructions of exoskeletons. Barták (2020) described Yantaromyiidae, a new family of Diptera, using also X-ray microtomography models. However, the conditions of Paleogene Europe, slowly surfacing from the seas, gave rise to more than one amber deposits. The Bitterfeld amber, despite some common properties, can be truly distinguished from Baltic amber and is also supposed to be younger, late Oligocene (Wolfe et al. 2016). The Ukrainian Rovno amber is older, comes from the late Eocene so its age is closest to Baltic amber, but their faunas do not match (Perkovsky et al. 2003, Perkovsky et al. 2007). In contrast, the French amber from Oise in Paris basin, is ca. 53 million year old, which corresponds to Ypresian of early Eocene. Hence, it is the oldest of the main European amber deposits (Brasero et al. 2009). In all of these ambers, some remarkable fossil specimens have been discovered.

Looking far away from Europe, an interesting Oligocene/Miocene deposit found in New Zealand was introduced by Schmidt et al. (2018). It contains diverse arthropod fauna and fungi, including resinicolous and predatory species. Previously known Chiapas amber deposit (Mexico) was suggested as Oligocene/Miocene age in 1960's (Langenheim et al.1967) and nothing much has changed since then. On the contrary, the Miocene (20 - 15 mya) age of Dominican amber (Iturralde-Vinent & MacPhee 2019), which is being intensively studied, was agreed recently.

1. 2. – Occurrence of amber in the Czech Republic
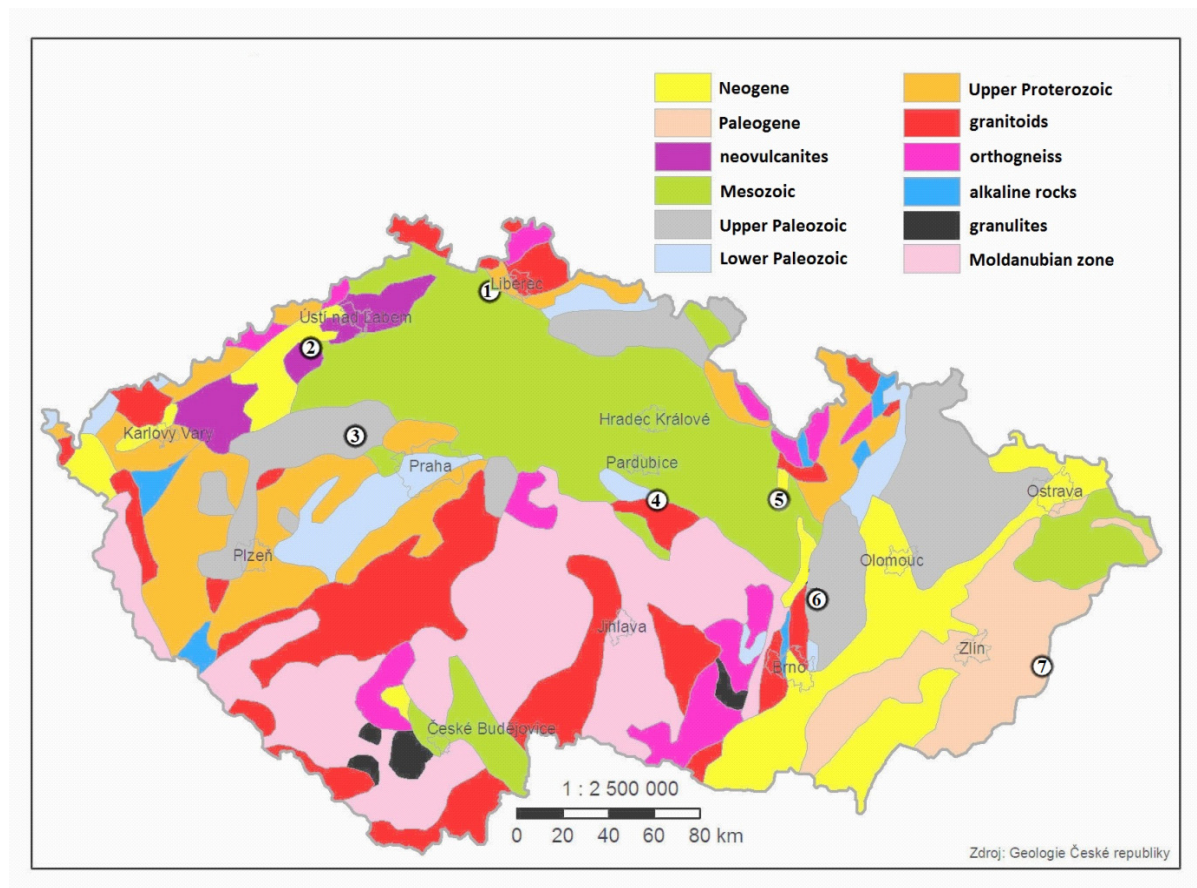
Fig. 4. – Notable amber deposits in the Czech Republic marked in simplified geological map: **1** – Křížany, **2** – Bílina, **3** – Nové Strašecí and Přílepy, **4** – Skutíčko, **5** – surroundings of Moravská Třebová, **6** – Valchov and Chrudichromy, **7** – Študlov; map after Hájková & Svobodová (2017), modified.

In the Czech Republic, coutry with such diverse geological settings, there are several known localities with occurrence of fossil resins **(fig. 4.)**. In northern Bohemia, the Cretaceous amber of Cenomanian age has been collected by Havelcová et al. (2014) in Křížany [1]. It is opaque, dark brown colour, found in proximity of a uranium mine (Havelcová et al. 2016).

Another type of fossil resin, called Duxite, can be found in lignite layers next to Bílina [2], where lignite is being mined. Its origins, however, seem to correspond to the lower Miocene, making Duxite stratigraphically the youngest of Czech resins (Havelcová et al. 2014). Its colour is brown, but not always fully opaque.

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Amber appears also in black clays next to Nové Strašecí [3] in central Bohemia. As well as the two previously mentioned ambers, it is brown and partly transparent as Duxit and probably Cenomanian (Havelcová et al. 2014). The village Přílepy [3], which lies only ca. 20 km far away from Nové Strašecí, is noteworthy for orange fossil resin, occurring in coaly slates and geochemically investigated by Jehlička et al. (2004). According to these authors, its age is Carboniferous (Westphalian stage). Unfortunately, this interesting resin has not attracted much attention. If the Westphalian age (around 307 Ma) is confirmed, the Czech Republic would host one of the oldest ambers in the world.

Further historical Cretaceous locality is called Skutíčko [4] near Chrudim. Amber from this site is often dark red colour dated to Cenomanian, as well as most of other Cretaceous ambers from the Czechia (Jehlička et al. 2004).

Further amber localities are close to Moravská Třebová [5]: Březina, Hřebeč or Nová ves (Streibl et al. 1976). Their age is corresponds to Cenomanian (Jehlička et al. 2004).

Valchovite found in Valchov and Chrudichromy [6] has been the best known Czech amber so far. Larger pieces were even often sold as objects of trade. Together with some previous ones, this light brown resin is dated to the Cenomanian (Havelcová et al. 2014).

While there are some mysterious cases like Carboniferous resin from Přílepy, most of the Czech ambers are confirmed as from Cenomanian. The simplified geological map used above certainly does not show enough detail, but provides an image sufficient to note that almost all Czech amber deposits lie somewhere on the borderline of Czech Cretaceous basin (see **fig. 4.**). During Cenomanian, mainland was reduced relatively in behalf of the sea. This fact could mean the increased occurence of promising ecosystems of variable salinity, shallow seas, estuaries and coastal swamps in region of borders of the Czech Cretaceous basin (Čech et al. 2005).

But there is still something more to note: While all previously described localities lie in the Bohemian Massif, which forms majority of the area of the Czech Republic, the only Študlov [7] is placed in zone of the Western Carpathians, which underwent their crucial formation during Cenozoic (Plašienka et al. 1997). If we disregard the national borders, and notice rather the geomorphology, there is at least one amber deposit, which should not escape our attention: Orava-Podhale Paleogene basin in Central Western

Carpathians. The amber was found in late-Oligocene deep water deposits.in the territory of Poland. The analyses suggest Araucarian origin of the resin. The amber contains fungal microinclusions and plant tissues and was exposed to wildfires and temperatures of almost 1000°C (Kotulová et al. 2019).

1. 3. – Locality Študlov

In past years, amber from Moravian locality Študlov has been collected by Jakub Prokop and his students and colleagues from Faculty of Science at Charles University. Študlov is the most promising Czech amber deposit, clearly differing from the others, which lie in Bohemian Massif. It has been the only Czech amber containing biological inclusions so far and it is supposed to originate in Eocene (Mátl et al. 1999, Havelcová et al. 2019). Havelcová et al. (2014) compared pyrograms of several Czech fossil resins and found some similar chemical components (borneol, cycloalkanes, and cadalene isomers) in the Cretaceous resins and Študlov amber. Due to these findings, the authors suggest that the plant producer of these resins, incl. Študlov amber, was common.

The Eocene age of the amber-bearing sediments was stated already by Peřinka (1905). According to Bokr (2009), geological subsoil of the locality "V Lázkách", where the amber is being found, is mostly composed of Paleogene sediments called Bystrica unit, with an exception of Holocene fluvial sediments alongside the Brumovka stream **(fig. 5.)**. There is a distinct sandstone-claystone layer (also called flysh) on the northern hillside of this part of White Carpathians, most likely belonging to the lower Eocene. The Bystrica unit belongs to Paleocene-Eocene Magura belt of Outer Western Carpatians (Plašienka et al. 1997).

The deposit itself has been known to locals for decades, and nowadays it is easily accessible by car. Many collectors visited the locality and attempted to gain the amber not only for scientific purposes, but also basically for its visual qualities, so it can not be estimated, how large amount of scientifically valuable inclusions stays undiscovered or undescribed until now, in private collections. Museum of Valašské Klobouky owns tens of amber pieces, usually not more than 2 cm in diameter, but no fossil organisms has been found inside them. Another museum of Valašský region in Vsetín posseses about 20 pieces of amber of similar diameter as the previously mentioned, without recorded evidence o fossil organisms.

At least two localities have been mentioned as amber-bearing in proximity of Študlov: V Lázkách, formerly called also "V Potocích", "V Akátí" or "Staškovo" and "Na Příkrém" (Kruťa 1944, cited in Mátl et al. 1999). The second locality, which will be here called "V Lázkách", seems more promising, bearing amber of higher quality and quantity, than "Na Příkrém". A few other findings of small amber pieces were made nearby, especially in mid Eocene sandstones of Bystrická unit (Mahel et al. 1962, cited in Mátl et al. 1999). Ručka & Sláma (1997), cited in Mátl et al. (1999) continued collecting at the locality "V Lázkách" to gain kilograms of newly found amber, which lay in coal slate layer in usually lenticular sockets. The amber pieces were up to 8 cm long and contained fossil arthropods.

The amber-bearing layers do not lie in horizontal position. They are transversally furrowed. The significant 30-50 cm thick dark-grey/black layers of claystone-sandstone, which mostly contain amber, need to be searched under 0.5 m thick layer of lighter-colored sandstones (Mátl et al. 1999). The same authors also notice positive correlation between occurence of coal and amber and lesser quality of amber found in close connection to coal. The amber itself is said to gain various shapes, some of them imply origin under tree bark or in inner spaces of tree trunk, while others, shaped like a dropet or a "straw", are typical for contact with external conditions. Samples of amber underwent Rock-Eval Pyrolysis, which indicated that Študlov resin passed through phase of higher temperature and had to be buried deeper in comparsion to Baltic amber. GC-MS analysis showed the presence of oleanane, which would suggest an angiosperm origin of the resin and fact that it is younger than Upper Cretaceous. In contrast, Havelcová et al. (2019) considered gymnosperm source plant as more likely.
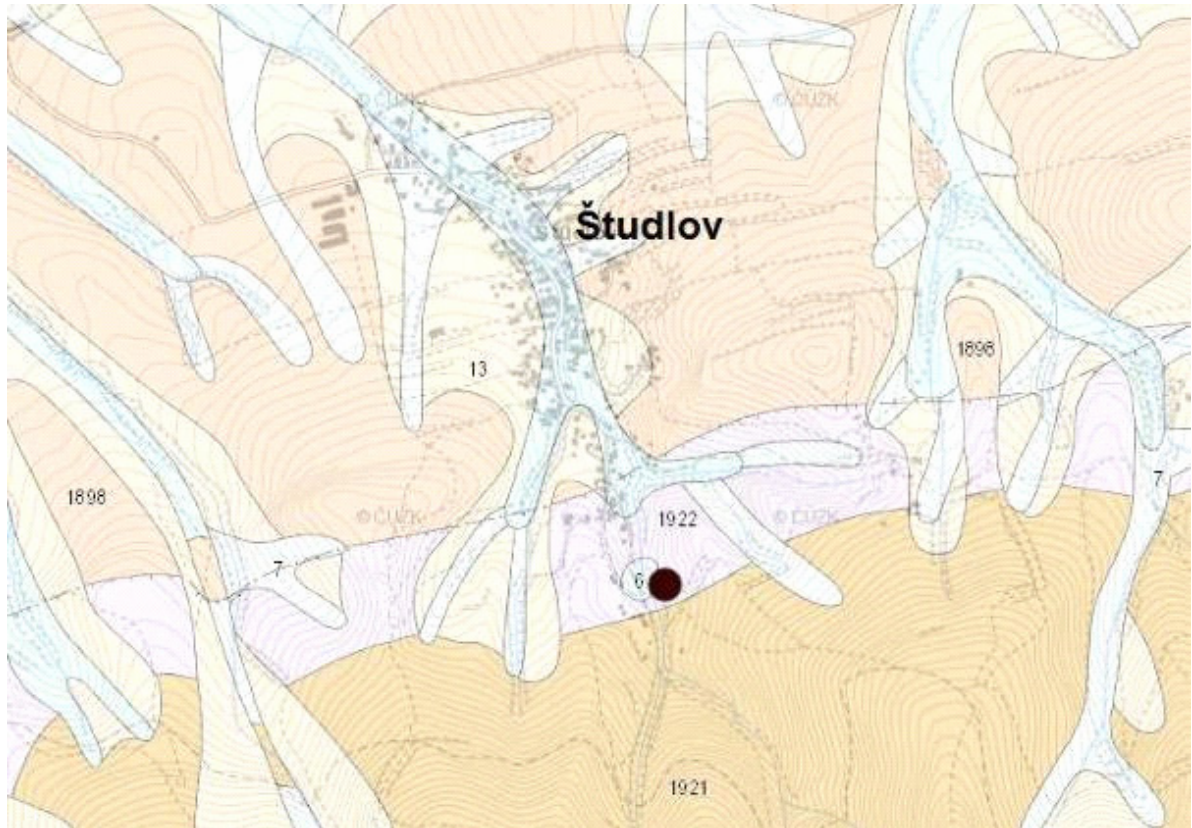
Fig. 5. – Detailed geological map of Študlov with indication of locality "V Lázkách". By brown dot. Light violet colour shows the Bystrica unit (no. 1922) on northern hillside of White Carpathians, followed by Paleogene sandstones, claystones and marlstones of Beloveža unit represented by light orange colour (no. 1922) and on the other side adjacent sandstones and claystones of Eocene and Oligocene represented by light pink colour (no. 1898). The other numbers represent Holocene sediments. The map taken from Bokr (2009).

2. Goals

The main goals of the present diploma thesis:

- To provide the first overview of biological inclusions preserved in Študlov amber (White Carpathian Mts.)

- To demonstrate significant species found in the Študlov amber inclusions compared to the related extant or fossil taxa from other world amber deposits.

- To discuss the age of Študlov amber, using the new findings and the previously published data from different fields.

- To outline the plant producer of Študlov resin and estimate the conditions that prevailed in the ancient habitat.

3. Materials and methods

The working process can be divided into three main partial tasks: amber digging, cleaning and photographic documentation of the samples. The digging works took place *in situ*, at the locality V Lázkách. All other tasks took place at Charles University in Prague at the Department of Zoology; Faculty of science, between the years 2017-2020.

3. 1. – Collecting and separation on sieves

The collecting efforts were initiated by Jakub Prokop, who visits the locality "V Lázkách" almost annually, for more than two decades.

"V Lázkách" lies in the Zlín region in eastern Moravia, at the foot of the White Carpathians, ca. 49.1553958N, 18.0883589E. All amber used as a study material for this thesis has been collected there. It is situated at the south-eastern part of the village Študlov. Its triangular shape is bounded by the Brumovka stream in the west, crest of a nameless hill in the east and a forest road lying south, rising from the stream to the hill crest **(fig. 6.)**. Most of the territory lies in altitude of 560 m. with maximal altitude difference of 110 meters, measured from Brumovka. The amber is being found in shallow pits, mostly excavated by the previous collectors. It is tricky to open new pits, since there is no guarantee of finding amber, but the experienced eye can sometimes track the layers of bluish claystone, promising the occurrence of coal and associated amber resin.

During past twenty years, many colleagues and students, mostly from Charles University's Entomology research group visited the locality V Lázkách, accessible by car, under guidance of Jakub Prokop in order to collect amber. The digging efforts were executed with pickaxes, shovels, hammers and chisels **(fig. 7.)**. Once the coal layers with co-occuring claystones was found, the soil was dug out put into buckets and transported downwards to the brook. The washing process on sieves followed **(fig. 8.)**. The sediments were poured onto stainless sieves 30 cm Ø in appropriate amounts and washed by water from the brook. As the sediments are being washed away, raw amber appears. It is than collected into test tubes and prepared for further studies.

Fig. 6. – Map of south-eastern part of locality "V Lázkách" with blue line representing the Brumovka stream, orange dot showing the approximate position of amber outcrops in coniferous forest and violet dot showing the washing place.
Source of map: https://mapy.cz/zakladni?x=18.0874491&y=49.1554934&z=19&base=ophoto

Fig. 7. - Michal Tkoč digging the coal-claystone layer with fossil resin content.

Fig. 8. - Martina Pecharová washing amber on sieves and collecting raw amber.

3. 2. – Cleaning and polishing

Right after the amber is collected, its low transparency does not usually allow observing and studying its inclusions. Piece after piece, the amber was processed at Department of Zoology. Amber from the test tubes was once more washed by water flow after putting onto stainless sieve, in order to get rid of the rest of the clay. Eventually a soft brush was used. Each piece was then wetted with water, increasing its transparency, and investigated with Nikon SMZ 745T stereomicroscope. Sometimes the amber showed no presence of inclusions even without further cleaning and polishing, and was immediately separated aside. The suspicious samples together with those containing inclusions were put in boxes determined for polishing process.

The polishing of amber was executed with wetted polishing papers: Carbonidum electrite 145 for raw polishing, Struers SIC # P1200 for most of the polishing process

and Struers SIC #P 4000 for fine polishing. In some cases, the polishing machine Crystal Master 8 (CM8-PLUS) was used, but careful manual polishing seemed to bring better results. The polishing efforts had to adapt each single piece, because straw-shaped fragments have to be treated different as flat ones. Large, stale amber pieces often fell apart when polished, but inclusions seldom occurred in those. The polishing process was controlled with Leica S9D stereomicroscope with attached Canon EOS 550D camera. All collected amber, the raw and the polished pieces, has now been stored in the collection of Department of Zoology at Faculty of Science, Charles University in Prague. There is about 400 g of controlled raw amber and about 60 g of polished amber containing biological inclusions.

3. 3. – Optical devices and visualisation

After polishing to reach the highest transparency possible and thinnest sample possible, the amber pieces containing biological inclusions could be photographed. The photographs were taken with Olympus BX40 optical microscope using Canon EOS 550D camera and UIS2 objective lenses 40x/0.65. Then the photographs were completed with Zerene Stacker Pro 1.04 software with "Pmax" or "Dmap" stacking. However, only 50% of samples containing inclusions were appropriate for photographic documentation. The remaining pieces were either too cracky, either contained too much air bubbles, either were too thick. The final photographs were in some cases edited (color corrections, brightness, contrast) with IrfanView 4.52 64bit.

All drawings were made using tracing-paper and photographs of the inclusions, using Marvy Uchida "For drawing" black liners 0.03, 0.05, 0.1 and 0.2. The drawings were edited with GIMP (GNU image manipulation program) 2.10.12.

The measurements were made either under Leica S9D stereomicroscope, either with Olympus BX40 optical microscope using micrometer (0.01mm) grid scale for stereomicroscopes.

4. Results

So far, Študlov amber has been the only resinous material from the Czech Republic, which has the real potential to contribute to our knowledge about Paleogene biota. The total number of 263 samples can be mostly divided into following taxonomical groups: Plantae, Arthropoda and Fungi (see the electronic list of amber specimens). Some inclusions, which were difficult to assign even to the high rank taxa, will be also demonstrated in this chapter. Along with these organic inclusions, numbers of pseudoinclusions were present, such as bubbles, discoidal surfaces or differently shaped cracks. A few insect inclusions have already been described by Jakub Prokop, André Nel and Michal Tkoč and will be shown below.

4. 1. – Plantae

Various wood remains can be often found in Študlov amber. There is also an inconsiderable amount of plant hairs trapped in the resin. Other plant inclusions are rare, but valuable, as the vegetation shapes our visions of ancient ecosystems. In a few amber pieces, small plant inclusions appear. They could be called "collapsed caps" **(fig. 11. F)**, and most probably they represent remains of fern or bryophyte spores.

4. 1. 1. – Bryophyta

Family indet. (fig. 9. – A.)

Material. No. 55 – moss fragment at the edge of transparent amber piece without other distinct syninclusions, but with hint of another, very damaged organic inclusion on the opposite side.

Description. This single Bryophyte specimen contains a moss gametophyte fragment of cauloide with two rows of leaves (phylloids) - (see **fig. 9. – A**). The fragment is ca. 800 μm long with phylloids up to 500 μm long, widest at base, without distinct midribs. Leaves single-layered, slightly serrate on edges, ended with a sharp tip.

Discussion. Distal parts of leaves are damaged and they could have been eaten by some herbivores. The fragment does not come from the terminal parts of moss plant. Its shape, lacking supporting structures, indicates pleurocarpous life strategy. But it is only an ecological adaptation; these lateral-growing mosses do not form any phylogenetic unit.

The presence of bryophyte remains in amber has been relatively rarely documented in a worldwide scale, except some notable moss community known from the Baltic amber (Heinrichs et al. 2014) or a Bryopside fossils from the Cretaceous deposits like Taimyr (Ignatov et al. 2016) and Myanmar (Heinrichs et al. 2014). The Dominican amber is also rich in moss inclusions. Frahm & Newton (2005) described 18 new moss species including *Mniomalia viridis* which resembles our specimen with its single layered phylloids and similar size, *Mniomalia* has been supposed to belong into order Hookeriales (Bryopsida). However, it would be necessary to find a larger moss fragment with sporophyte to determine this moss.

4. 1. 2. – Wood and remains of woody tissue of Spermatophyta

In more than quarter of all amber samples (see electronic list of inclusions), some remains of plant tissue were present. Usually it could not be further studied because of their poor preservation, but in about fifteen cases, wood cells and some of their secondary structures were discernible enough to provide a hint of the embedded plant's origin. A few of the most notable ones will be mentioned here.

In specimen no. 33 (**fig. 9. – B)**, a wood imprint appears on semitransparent amber piece. Surface pattern of this 1 cm long piece exhibits regular, parallel horizontal furrows, 0.5 mm high. No structure of wood cells can be distinguished. Under each hollow, an immersed oblong socket reaches the inner space.

The specimen no. 233 (**fig. 9. – C-E)** in an exceptional case of fossilized gymnosperm twig. It is a cylindrical part of woody stem, mostly opaque, partially pervaded by resin. Tangential and transverse sections were well visible, however to see the radial plane, the sample had to be cut in half, and thereafter one half could be polished to gain radial view. The fragment has 2.9 mm Ø and was originally 1.1 cm long. Tangential section is composed of 7 growth rings.
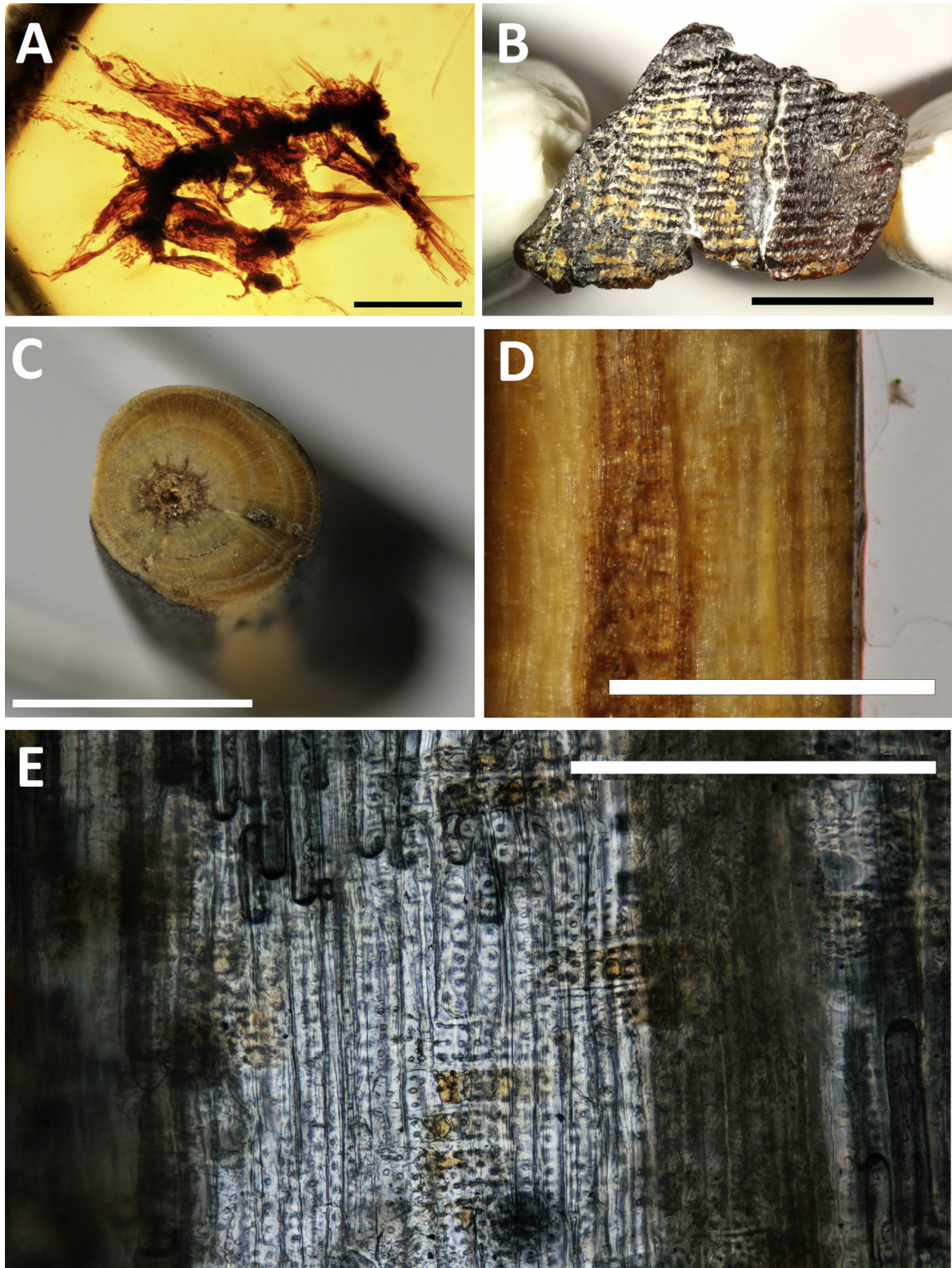
Fig. 9. – **A**, pleurocarpous moss from no. 55, scale bar: 200 μm. **B**, storied rays from no. 33, scale bar: 5 mm. **C-E**, gymnosperm twig (Cupressaceae), no. 233, scale bar C: 3 mm, scale bar D: 2 mm, scale bar E: 200 μm.

The specimen no. 16 **(fig. 10. – C)** contains woody tissue and thick-wall fungal cells. The wood structure is damaged on tangential section. Most of the area there the wood cells once laid is hollow, but in some parts the wood structure is well preserved. Rays seem to be seriate with 2 or 3 rows of cells, up to 250 μm long. Next to the layer of wood tissue, there are some thick-walled, most probably fungal spores.

Thick clusters of gymnosperm wood are preserved in specimen no. 20, in larger, transparent amber piece without syninclusions. Two ca. 2 mm long, dark clusters of wood cells lie trapped in resin close to each other. Borders of each cluster seem to be sharp and distinct, as the cells are cut in lines.

In specimen no. 29 **(fig. 10. – D)**, clusters of small sections of gymnosperm wood occur in transparent amber piece without syninclusions. These wood remains vary in size and forms. There are some composed of only a few cells, as well as larger, more compact clusters with distinct edges (similar to no. 20). One fine ray with 9 cells is apparent on tangential section.

Specimen no. 95 **(fig. 10. – E.; F)**, contains various woody tissues. It is an interesting mixture of longitudinal wood cells. The cells are truly long (some up to 1mm) and also forming long parallel groups (lines). But there are also shorter cells, some almost as long as wide, forming either rows consecutively (see **fig. 10. – F**), or adjacent rows. In case of forming short adjacent rows, the cells are flat.

Single wood cells and structure resembling an angiosperm vessel member are preserved in specimen no. 114. Wood cells in this specimen occur only as singles or small groups. By the edge, a single angiosperm vessel member appears 500 μm long and 120 μm wide, with typical surface ornamentation. Three longitudinal wood cells lie next to the vessel member.

In next specimen, no. 115 **(fig. 10. – A)**, there is a layer of dim wood tissue on the surface of clear orange amber piece without syninclusions. Rays are 200 μm long, composed of ca.10 cells. There is no material apparent under this layer, and the layer itself creates surface to the amber piece.

The last specimen is no. 246 **(fig. 10. – G)**, with wood cells accompanied by thick-walled fungal cells in transparent amber piece. The woody tissue is apparent on

tangential section and containins polyseriate (2-4 rows) rays. The slightly concave layer seems to be a negative imprint of gymnosperm tangential wood.

> **Fig. 10.** – Examples of some woody tissue fossils. **A**, tangential section with single-row gymnosperm rays from specimen no. 115, scale bar: 150 μm. **B**, another tangential section, specimen no. 246, scale bar: 200 μm. **C**, disintegrated wood, also tangential section. specimen no. 16, scale bar: 500 μm. **D**, wood tissue cluster from specimen no. 29, scale bar: 100 μm. **E**, a group of fibres from specimen no. 95, scale bar: 100 μm. **F**, antoher wood cells from specimen no. 95, scale bar: 200 μm. **G**, combined wood tissue from specimen no. 241, scale bar: 200 μm.
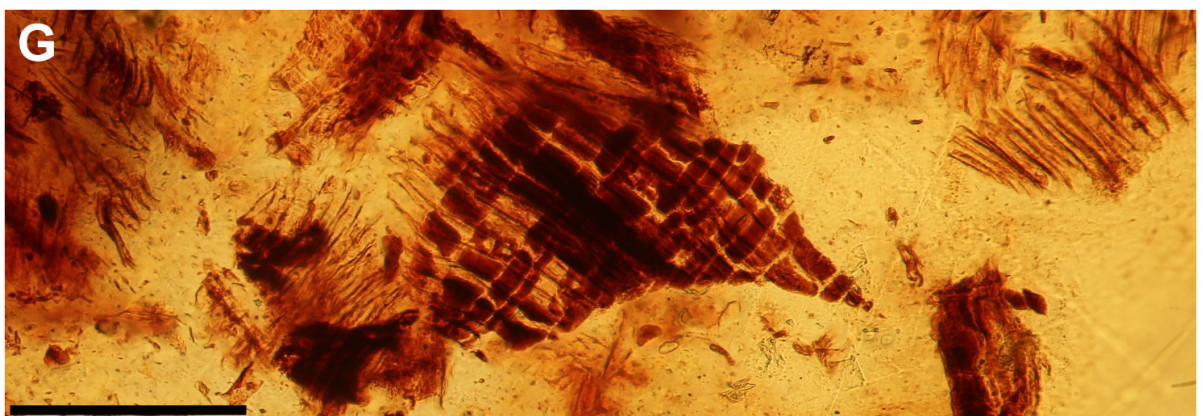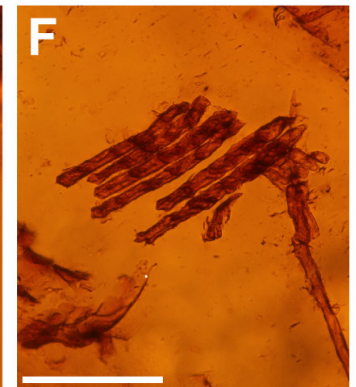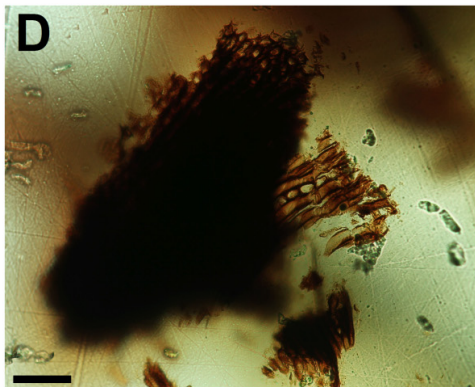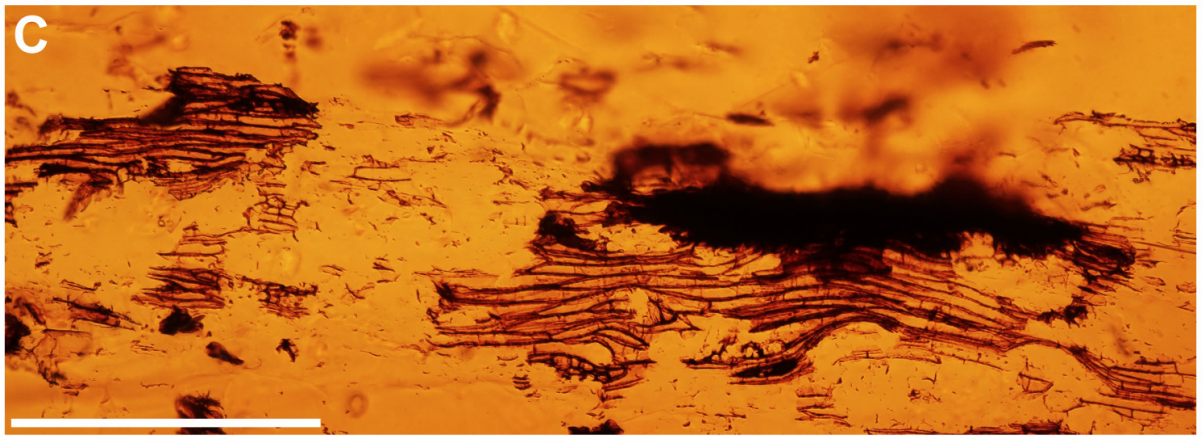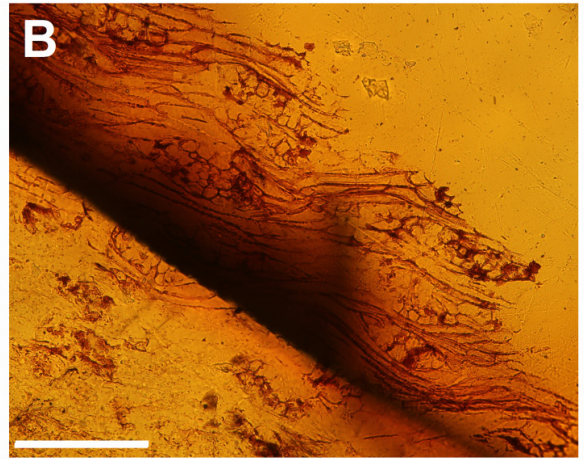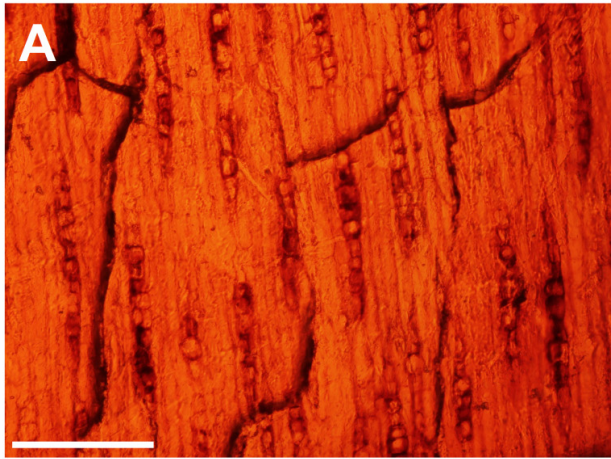
Summary: Wood in Študlov amber.

It would be unreasonable to try to determine each sample of wood in Študlov amber. The remarkable feature here is the diversity of wood preservation. Most of the wood tissue correspond to gymnosperms, with some suspicious cases like no. 246, or the self-evident angiosperm vessel member in specimen no. 114. In at least two cases (no. 16 and no. 246), tangential layer of wood cells is accompanied by thick-wall clusters of fungal cells. Judged by the damage of wood, it is possible that the fungi grew on the wood cells, but then the thin-wall hyphae did not preserve in amber, in contrast to the resistant spores (thick-wall cells). Further similar cases will be shown in chapter "Fungi".

In a few samples, like no. 20 and no. 29, clusters of wood cells have distinct edges and they even seem like being cut off. Several explanations exist, e.g.: these clusters once could serve as food of an unknown herbivore. Then they fell to fresh resin and preserved. But the cracks on surface of no. 246 imply another explanation - as new resin is being produced by the tree, the resin flow rips the wood layer off, leaving a "messy" look to what remains.

So far, minimal amount of syninclusions of wood tissue with other biological material have been discovered in Študlov amber, which leads to conviction that a large portion of the amber originated in inner (gymnosperm) tissues of the producer and had no chance to interact with the environment (except fungi), until it began to fossilize. Nevertheless, these woody tissues can emerge both like a surface imprint and like an inner fossil as well.

Woody tissue is rather rarely documented from amber deposits. A question offers itself: is the fossil wood in amber so rare, or just overlooked? It seems quite hard to find a well preserved woody tissue in amber. Better results have been often gained rather from related coal material (Néraudeau et al. 2017). The oldest example of a woody tissue embedded in amber comes from the lower Jurassic of northern Italy. The tissue is curious, hardly comparable with any other vascular plant tissue ever found in amber, but at least it shows some signs of araucarian wood patterns (Neri et al. 2017). The problem is that these specimens do not give an opportunity to examine all three sections at once, which is crucial for wood determination. More likely the amber wood is represented by

the clusters of wood cells, or sometimes even particles that passed the digestive system of small herbivores (Nuorteva & Kinnunen 2008). This could be the case of specimen no. 20.

Specimen no. 33 is unique with its traces, which may occur when the xylem rays lie in regular distances and simultaneously, when the viewer watches tangential level of woody tissues, but not necessarily tangential section. Meier (2008) describes these furrows as "storied rays" and the pattern as "ripple marks" and calls them more typical for extant tropical woody plants. They can be formed both by angiosperms and gymnosperms. De Franceschi & De Ploëg (2003) found simillar patterns on angiosperm wood of the genus *Aulacoxylon* (Fabaceae, Leguminosae), which is supposed to be a producer of resin in early Eocene amber from the Paris basin.

The most interesting wood remain from Študlov amber is represented by a twig, no. 223. Based on the apperance of cross field pitting, which is taxodioid (see Wiedenhoeft & Miller 2005) (Sakala 2019, pers. comm.), most of the Pinales families can be excluded, while Cupressaceae s.l. can be the original plant source. Within Cupressaceae, these are the characters after Román-Jordán et al. (2017), which support the assignment of the fossil twig to *Glyptostrobus* Endl.: tracheid pittings in radial walls uniseriate or biseriate, pits without notched borders, axial parenchyma present, axial parenchyma arrangement tangentially zonate, ray tracheids absent or very rare, cross fields taxodioid. According to Esteban et al. (2004), who compared 352 conifer species from the aspect of their wood anatomy, these characters are shared within *Glyptostrobus pensilis* (Staunton ex D.Don) K.Koch, 1873 and the Študlov specimen: Rays uniseriate, ray height 1-15 cells, cross field pitting taxodioid, 1 to 4 pits per cross field, well defined growth rings, bordered pits present of the tangential walls of the axial tracheids, uniseriate or biseriate bordered pits on the radial walls of the axial tracheids.

There is also the specimen no. 115 (**fig. 10 – A**), showing similar arrangement of uniseriate rays on radial view, as *Glyptostrobus*.

The twig is partially permeated with resin, but the pith remains free of resin. This is an interesting fact itself - if the twig fell into fresh resin from a tree and was captured there, it would surely be soon poured all over. However, when the twig fragment was found, it did not show any covering with amber, not even at the centers of the transverse

sections. The pith remained soft, easy to damage and free of resin on both ends of the cylindrical twig fragment, and of course, also in deeper sections of the specimen, after being cut.

In contrast, if the plant produced the resin itself, only the adjacent and outer tissue would be affected. So the plant from which the twig comes from could be the amber source plant. *Glytostrobus* would be a suitable plant producer. Known from Early Cretaceous Aptian of Canada and Greenland, it spread into Eurasia in Paleogene. It is supposed to dominate the swamp ecosystems of Central European Depression during Neogene, later however decreased its abundance in Eurasia and North America, persisting only in China, growing in waterlogged ecosystems. *Glyptostrobus* preferred middle to high altitudes and was negatively affected by aridization and cooling in Oligocene and later (LePage 2007). So, even if *Glyptostrobus* was just one of the resiniferous trees, not directly the plant producer of Študlov amber, and its twig fragment preserved in the strata by a chance, some estimations about the paleoecosystem can be made.

However, not enough direct divergencies were found between the wood anatomy of Študlov gymnosperm twig and the extinct genus *Doliostrobus* Marion, 1884 (Doliostrobaceae), which also should be kept in mind as the alternative taxon for the fossilised twig identity.

The cupressoid twig contains extremely well-preserved cells and tissues, described from Baltic amber by Koller et al. (2005), and also shows common features with *Glyptostrobus*. Sadowski et al. (2017) analysed coniferous foliage from several Baltic amber collections and verified the occurrence of various gymnosperms such as *Calocedrus* and *Taxodium* (Cupressaceae), *Abies, Pinus, Pseudolarix or Nothotsuga* (Pinaceae) or *Cupressospermum* (Genitziaceae). This fact shows that the amber forests were hardly dominated by a single tree species. Rather they were a complex ecosystem with diverse vegetation.

4. 1. 3. – Angiosperm trichomes

Material. No. 22 – syninclusion of a nematode with a bifurcate plant trichome and remain of an insect exuvia in "straw"-like piece of amber with many other small organic inclusions (**fig. 11 – A**).

Discussion. Bifurcate trichome is the only plant hair in the sample, at least the only complete. Another one or two examples of such trichomes or any other distinctive plant tissues could help us to understand the context. Yet we can only suppose the shortest arm is the major, while the two long arms indeed are bifurcate, branching in U-shape. The whole trichome is probably single-celled.

Plant hairs acquire the most varied shapes and sizes. They have been known as frequent inclusions in Myanmar, Baltic and Dominican ambers and in many other world amber deposits. They are usually fragile enough to separate from the original plant and eventually get captured on sticky surface of fresh resin. It can not be said for sure, whether this plant hair has been preserved entirely, or if it only a part of even more-branched plant hair. The shape of the branching could possibly assign the fossil to Brassicaceae family, whose members use to have trichomes of similar shapes (Ančev & Goranova 2006), still with high level of uncertainty, caused by the fact that another 8 famillies - Acanthaceae, Amaranthaceae, Cneoraceae, Connaraceae, Convolvulaceae, Cornaceae, Malpighiaceae and Fagaceae, can have bifurcate trichomes as well (Metcalfe & Chalk 1979).

Material. No. 153 – A Stellate trichome in small clear amber piece without syninclusions (**fig. 11 – C**).

Description. Apparently better-preserved stellate hair with 11 arms. Probably coming from the different plant species than the specimen no. 1. It also is of larger size (about 300 μm Ø)

Discussion. Stellate trichomes were probably quite abundant as they are commonly preserved in various Cenozoic resins. Peñalver et al. (2007) noticed stellate-like trichomes in the Lower Cretaceous of Spanish amber; however those specimens are differently shaped (more tree-like than stellate). Stellate trichomes have been typically found in Baltic Eocene amber in remarkable quantities. Their origin can be attributed to

Fagaceae family and it is believed that these hairs grew on the surface of *Quercus* flower (Clark & Daly 2010). Enormously high amount of stellate trichomes occur in Burmese amber and escapes attention.
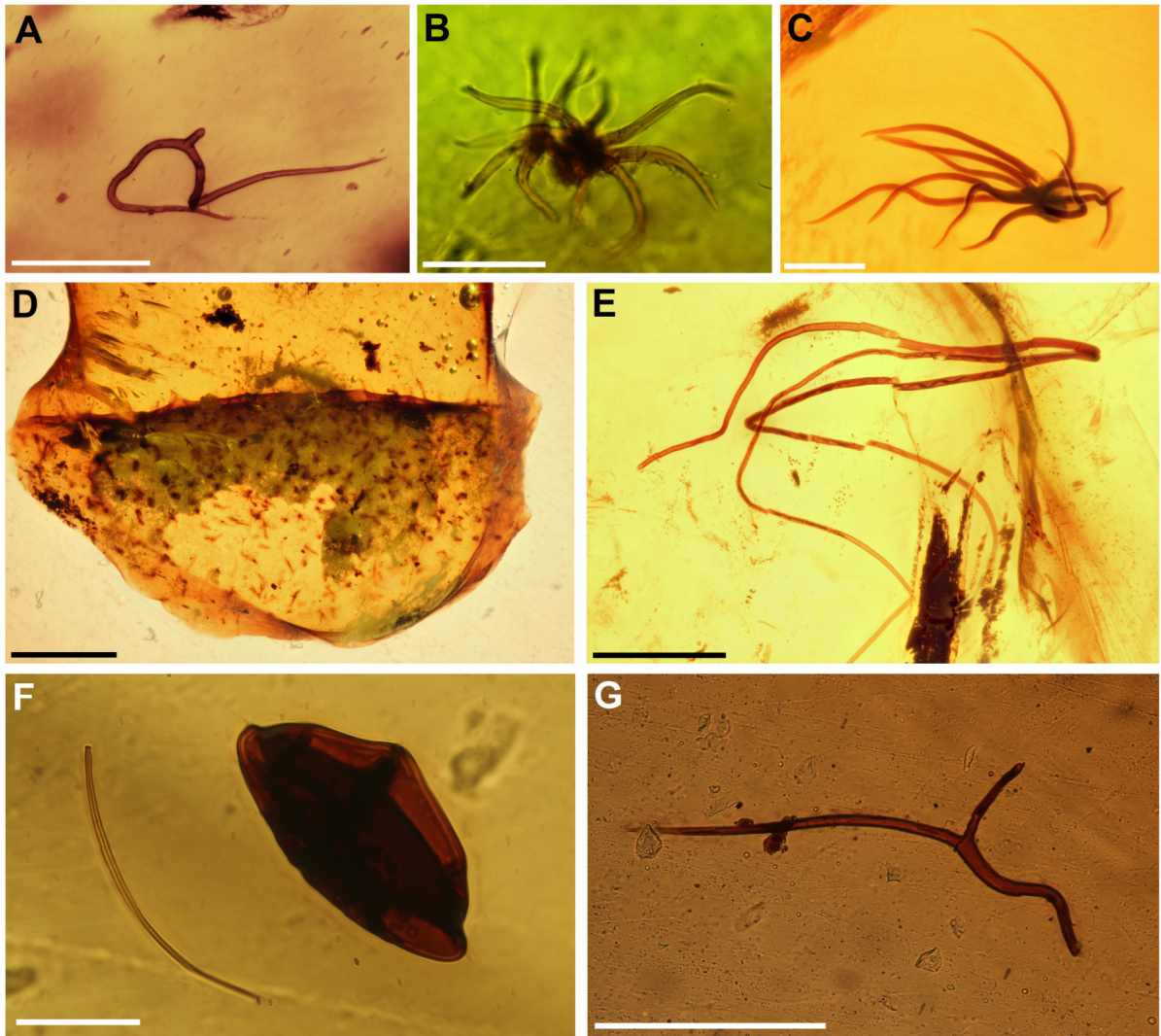
Fig. 11. – Trichomes from Študlov amber. **A**, bifurcate trichome from no. 22, scale bar: 200µm. **B**, minute stellate trichome from no. 1, scale bar: 50 µm. **C**, stellate trichome from no. 153, which is much larger than B, scale bar: 100 µm. **D**, plant surface embedded in amber with simple trichomes from no. 68, scale bar: 500 µm. **E**, tripartite trichome from no. 178, scale bar: 200 µm. **F**, simple trichome with unidentified plant structure from no. 83, scale bar: 50 µm. **G**, branched incomplete trichome from no. 245, scale bar: 250 µm.

4. 2. - Fungi

Subkingdom: Dikarya

Material. No. 176 – Clustered fungal spores in transparent amber piece, embedded together with remains of tenuous mycelia (**fig. 12. – A; B**).

Description. The spores are quite significantly pigmented, all about 50 μm long, regular, oval, some of them having central depression. They seem quite thin-walled, often being cracked. Black dots on spore surface can be artificial. The largest cluster contains about 25 spores. A single three-celled fungal formation, 20 μm, can also be found in this specimen.

Discussion. As the spores hold together, it is presumable, that their source was nearby. They even seem to rest on a surface that disintegrated. The spores did not germinate. None of them has a protuberance, nor a narrow section, which would imply conidiogenesis, so these are probably sexual spores.

Ascomycota

Material. No. 71 – Syinclusion of microsclerotia or microsclerotia-like pigmented cells with remains of woody tissue (**fig. 12. – C**).

Description. In this specimen, minute remains of woody tissue occur in one layer, and, adjacent to this hardly noticeable surface, fungal cells appear, scattered all over the plane. Each single one is about 35 μm long and they can either rest single, or form clusters of maximum about 10 cells.

Discussion. These cells do not seem regular enough to be called spores. Their unsteady shape and uneven pigmentation (sclerotisation) rather indicate the need of the fungus to produce a resistant stage on a plant surface. If there were any hyphae with thin cell walls, they probably disintegrated before the amber fully matured. Even the woody tissue's preservation has been limited to a few remains of cell walls. All these clusters of fungal cells could be, with certain caution, called "microsclerotia", which are fungal structures designated for spreading onto new surfaces and overcoming unfavorable conditions, especially in case of phytopathogenic fungi, and which combine less and more

pigmented cells (Song 2018). Similar, though not the same structures, has been observed for example within *Scleroconidioma sphagnicola* Tsuneda, Currah & Thormann, a Hyphomycete associated with *Sphagnum*, described by Tsuneda et al. (2000). By the way, this is another example when woody tissue can be found together with non-mycelial fungal structures in Študlov amber.

Material. No. 10 – Syninclusion of microsclerotia or microsclerotia-like pigmented cells with remains of woody tissue in flat, transparent amber piece (**fig. 12. – D**).

Description. The overall appearance of fungal structures in specimen no. 10 greatly reminds those of specimen no. 71. These cells are each about 50 μm long. They stay single or form clusters of tens of cells. Plant remains are slightly more distinct than in specimen no. 71, they also used to form a surface hosting these fungal structures. Except organic inclusions, this amber piece has notable inner structure with bubbly interface of resin layers.

Discussion. Life strategy of no. 10 and no. 71 were probably similar – colonizing of various plant surfaces and relying on resistant stages. Both of them could probably represent the ubiquitous Dothideomycetes, which have an inexhaustible amount of life strategies (Hyde et al. 2013) or at least Pezizomycotina, based on ecological characters of the fungi, rather than on morphology.

Material. No. 94 – Syninclusion of a female barklouse with a moss mite, an incomplete fly and fungal hyphae of at least 2 types in layered amber piece of high transparency and tenacity. The four inclusions are not in direct contact (**fig. 12. – E**).

Description. Minute fungal mycelia and germinating conidia lie in proximity of the barklouse remain. All fungal structures are max. 60 μm long and 10 μm wide.

Discussion. A typical conidium in this specimen is only 5 μm wide, 50 μm long and has 6 septa. The conidiophore could perish some time sooner, otherwise it would probably preserve. In **fig. 12. – E**, the conidium is captured when germinating. The translucent, thin-walled mycelium shows no significant features.

In case of certain *Pleospora* Rabenh. (1857) species (Pezizomycotina, Dothideomycetes), the conidia look alike – having long appendix and germinating from the opposite side, which closed to the conidiogenous cell. Conidia of these species have even been produced soon after a single ascospore germinates (Lucas & Webster 1964). Hyphae and conidia in Specimen no. 94 could be assigned to Dothideomycetes. Whole conidiophores of various Ascomycetes are not so rare in amber (Dörfelt & Schmidt 2007) and it is a shame that at least some did not preserve in študlov amber as well.

Material. No. 236 – Septate spores in small, transparent amber piece without syninclusions (**fig. 12. – F**).

Description. Each single spore is about 11 μm long and 9 μm wide. They seem relatively dark, but all of them have a clear septum. They occur as single spores, pairs, group of three, group of four – in the most typical case, or as more numerous groups. Usually they hold together in rows, with their longer sides adjacent, septa forming a line.

Discussion. These dark, regular spores, can be either called conidia, or ascospores. For instance, the phytopathogenic *Botryosphaeria sarmentorum* Phillips, Alves & Luque 2005 (Dothideomycetes) produces ascospores and conidia, both with one septum, both of very similar shape and size (Phillips et al. 2005).

Material. No. 48 – short septate hyphae in transparent amber piece, embedded in epoxy layer. Syninclusion with indistinct, layered organic matter. (**fig. 12. – G; H**).

Description. Thick-walled mycelia constricted to small septa seem to grow out of decomposed surfaces together with more subtle hyphae.

Discussion. Appearance of theses fungal structures, where subtle and thick hyphae combine, could indicate growth on a surface (for example tree surface). However, some distinctive structures as conidiophores would help to guess more about ecology or taxonomical position of these fungi.

In good conditions, even fine mycelial fibers can preserve, known from instance from Bitterfeld amber (Rikkinen & Poinar 2000), but more often, reproductive and resistant structures have much higher chance to persist (Rikkinen and Poinar 2001).
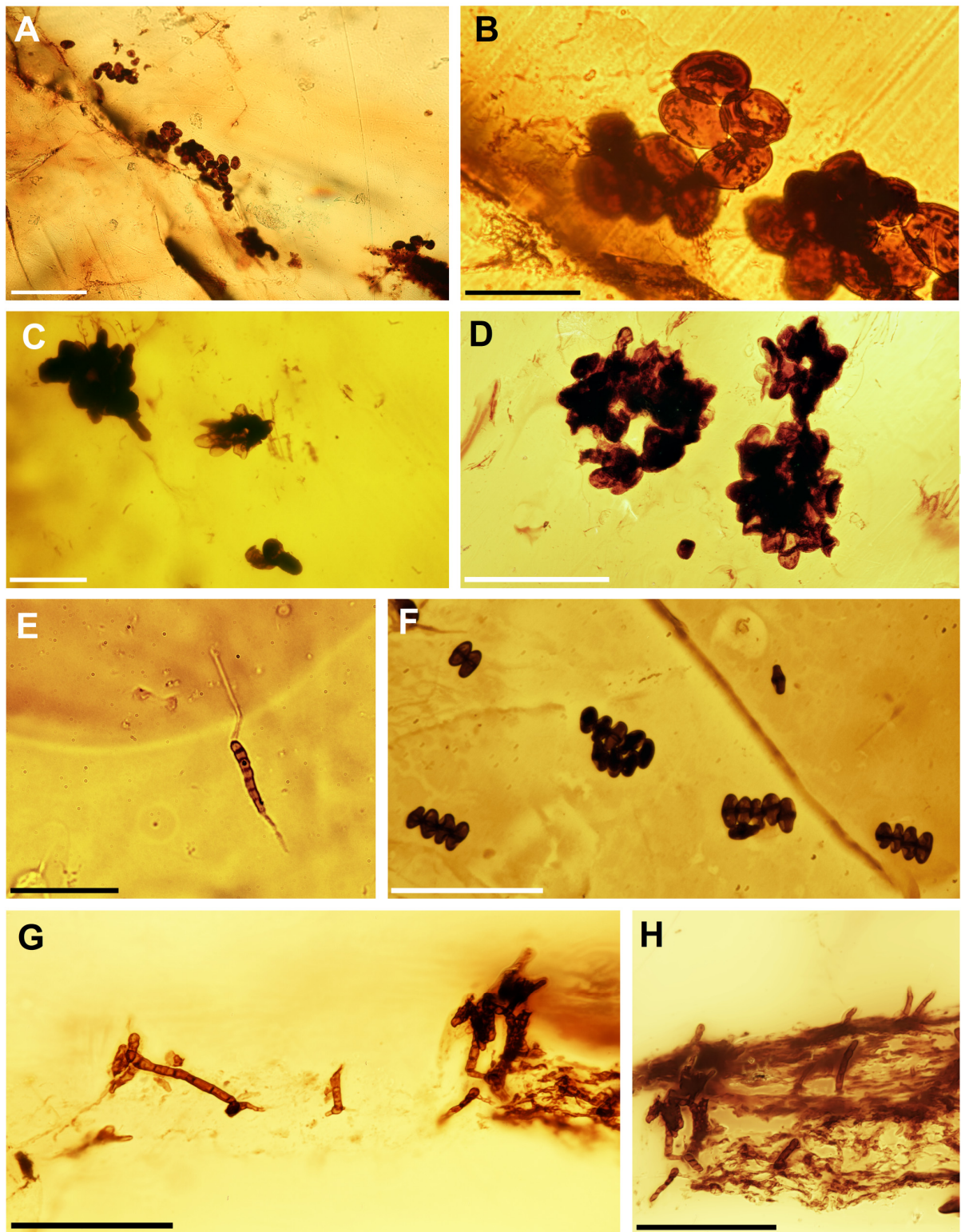
Fig. 12. – Fungal inclusions from Študlov amber. **A+B**, spores from no. 176, scale bar A: 40 μm, scale bar B: 50 μm. **C**, cell clusters from no. 71, scale bar: 100 μm. **D**, cell clusters from no. 10, scale bar: 200 μm. **E**, germinating conidium from no. 94, scale bar: 100 μm. **F**, spores from no. 236, scale bar: 100 μm. **G+H** – septate hyphae from no. 48, scale bars G+H: 100 μm.
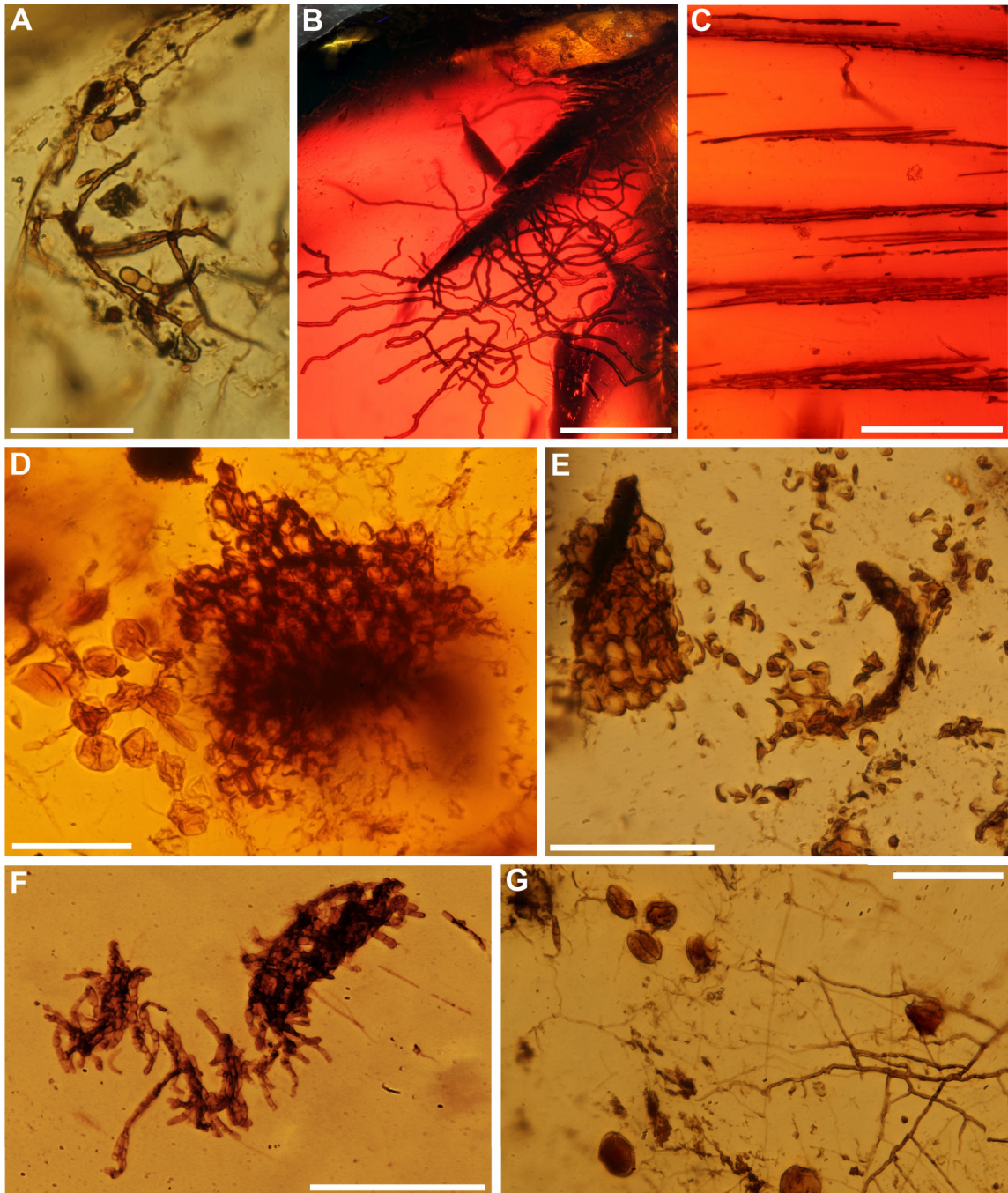
Fig. 13. – Fungi incertae sedis from Študlov amber. **A**, hyphae with thickened septated end from no. 235, scale bar: 5 μm. **B, C** – narrow tunnels left after decomposition of the original mycelium from no. 257– the fungus was probably growing on resin surface, B shows an upper view of one layer of hyphae, C shows layers in horizontal view, scale bar B: 25 μm, scale bar C: 20 μm. **D**, one of the organic microinclusions from no. 54, in which various fungal structure co-appear with these - probably plant - cells, scale bar: 10μm. **E,** similar structures as shiwn in D, specimen no. 229, scale bar: 10 μm**. F,** cluster of hyphae from no. 229, scale bar: 10 μm. **G,** hyphae and spores from no. 229, scale bar: 10 μm.
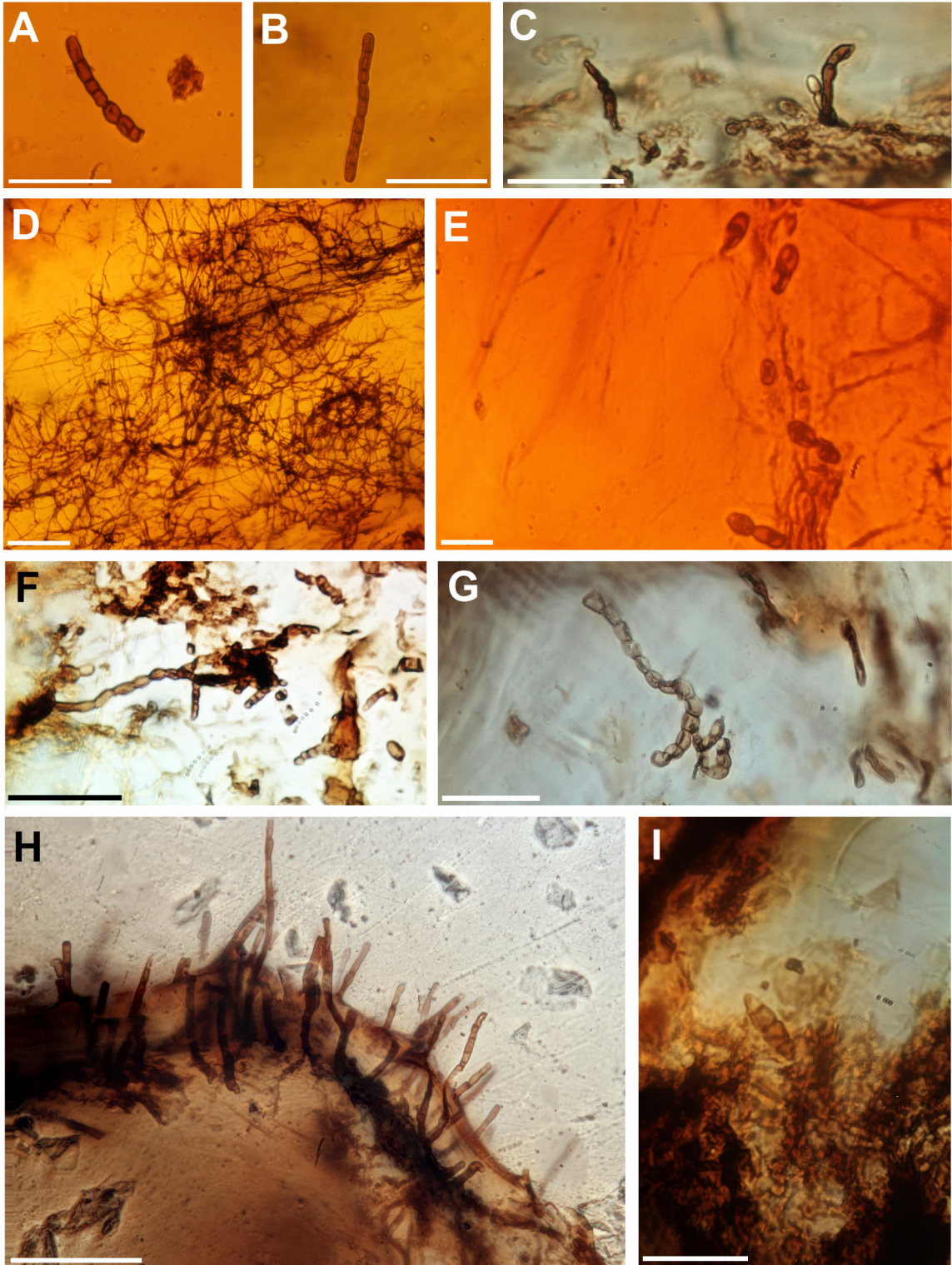
< Fig. 14. – Fungi incertae sedis from Študlov amber. **A+B**, short dark hyphae from no. 66, scale bar A: 5 μm, scale bar B: 5μm. **C**, mycelium growing on a surface, no. 90, scale bar: 5 μm. **D**, mycelia from no. 116, scale bar: 10 μm. **E**, collapsed spores, some with both transverse and longitudinal septum from no. 177, scale bar: 2 μm. **F**, conidiophore or similar structure from no. 226, scale bar: 5 μm. **G,** septate, less pigmented hypha from no. 226, scale bar: 5 μm. **H**, hyphae growing from a surface from no. 226, scale bar: 10μm. **I**, septate ascospore or conidium from no. 226, scale bar: 5 μm.

The overall diversity of amber fungi has been considerable, including even resinicolous species (Rikkinen & Poinar 2000). Also Študlov amber contains resinicolous mycelia (at least in specimen no. 125). However, only in a limited way - almost none amber fungi other than Ascomycetes or Basidiomycetes exist. It is supposed that fungi out of the subkingdom Dikarya have too subtle mycelia with too low level of sclerotisation. They are usually quickly growing and quickly decaying, not forming durable cells or hyphae.

Fungi have often been literally overlooked. While the most significant discoveries from amber can be observed by human eye, mycelia often grow in order of micrometers, which makes them difficult to see without high magnification. To observe an amber piece with a microscope, it is beneficial to attenuate the specimen as much as possible and not always is this operation possible. If all specimens of world amber non-fungal inclusions would be investigated again, lots of new discoveries would surely follow.

4. 3. – Arthropoda

Subphylum: Chelicerata

Class: Arachnida

Subclass: Acari

Superorder: Acariformes

Order: Oribatida

Suborder: Brachypylina Hull, 1918

Family indet. (fig. 15 - A).

Material. No. 94 - Syninclusion of a female barklouse with a moss mite, an incomplete fly and fungal hyphae of at least 2 types in layered amber piece of high transparency and tenacity. The four inclusions are not in direct contact.

Description. Body dorsoventrally flattened, 280 μm long, notogastral length 200 μm. Notogaster oval, elongated. Sensilla max. 45 μm long, clavate, sclerotised, placed at level of coxa II. The circumgastric scissure overlapping significantly to ventral side. Genital and anal shield (plate) apparent, not approached, anal shield 60 μm long. Femora of all four pairs of legs enlarged, the first two about half as thick as long, 40 μm long and 20 μm wide. Tibia I 30 μm long with a significant hump bearing at least 40 μm long solenidia. Elongated solenidia apparent also on tibia II. Tarsi tridactyle.

Discussion. This mite belongs to suborder Brachypylina (Oribatida), based on the following combination of characters after Walter (2006): Solenidia erect on distal leg segments, tridactyle tarsi, femora IV undivided, coxae I-IV contiguous, imagines with 4 pairs of legs, dorso-sejugal division into 2 shields, adults beetle-like with prodorsal trichobothriae, 1 pair of clavate (capitate) sensilla, capitulum withdrawn into head or camerosome.

Suborder: Brachypylina

Family indet. (fig. 15 - B).

Material. No. 227 – An oribatid mite preserved in clear amber piece without syninclusions. The amber is transparent, but containing plenty of parallel scratches.

Description. Body 265 μm long, length of idiosoma 200 μm. Body twice as long as wide in the widest place. Notogaster round, forming the slightly convex dorsal side of mite's body. Sensilla ca. 50 μm long, clavate, also placed at level o coxa II. Gnathosoma bearing several setae up to 50 μm long on dorsal side. Genital shield 35 μm Ø, placed at level of coxa IV. Anal shield placed terminally on ventral side. Mouthparts straight, compact, but with small protruding chelicera. Leg I with enlarged trochanter and femur, femur I 50 μm long and 25 μm wide. Genu I 13 μm long. Tibia I 40 μm long with solenidia 80 μm long. Tarsus I 30 μm long. Leg II with femur of same size and shape as leg I. Leg IV with large round trochanter. Femur IV not enlarged, 50 μm long. Tibia 55 μm long. One leg IV is complete, however the genu + tibia + tarsus of the second one lies apart. Tarsi tridactyle.

Discussion. This mite belongs to suborder Brachypylina (Oribatida) based on the combination of the following characters after Walter (2006): Solenidia erect on distal leg segments, tridactyle tarsi, femora IV undivided, imagines with 4 pairs of legs, dorso-sejugal division into 2 shields, genital shield postcoxal, adults beetle-like with prodorsal trichobothriae, 1 pair of clavate (capitate) sensilla, capitulum withdrawn into head or camerosome.

Suborder: ? Brachypylina
Family indet. (fig. 15 - C).
Material. No. 232 – An oribatid mite in transparent amber block without syninclusions.

Description. Body 220 μm long, notogaster 140 μm long. Gnathosoma with long conical orthognathous rostrum, probably suctorial, bearing the protruding chelicera and two pairs of long postcheliceral organs (palps and setae), of which the second pair is longer (ca. 25 μm). Ventral side without significant features, but there are clavate sensilla apparent on the dorsal side. Legs I seem to be modified, shortened, heading straight upwards, vertically to rest of the body. Legs II also raised upwards, but only coxae, trochanters and femora preserved. Legs III and IV with enlarged trochanters. Trochanters of legs III and IV protruding laterally. Only on the left side the legs preserved completely, raised upwards slightly, tridactyle tarsi apparent. On the right side the legs are preserved only to femora.

Discussion. This mite belongs to Oribatida based on the following combination of characters after Walter (2006): tridactyle tarsi, coxae I-IV contiguous, imagines with 4 pairs of legs, prodorsal trichobothriae, 1 pair of clavate (capitate) sensilla, genital shield postcoxal with trapdoor valves, pedipalps shorter than 5-segmented. There are too few signs to determine this fossil mite better, but presumably it falls into Brachypylina like the three others sharing the main morphological charcaters (suctorial rostrum, relatively short pedipalps) (Walter 2006).

Suborder: Brachypylina

Family indet. (fig. 15 - D).

Maretial. No. 103- An oribatid mite trapped between two resin layers of transparent amber piece without syninclusions.

Description. Body 280 μm long, round (almost as wide as long), compact, strongly sclerotised. Notogaster with pteromorphs. Gnathosoma conical, chelicera covered by layer of cuticle. There are four apparent pairs of setae, sticking out from the rostrum. The first pair is ca. 25 μm long, acompanying chelicera. The second pair is about 60 μm long, growing from small bulk on lateral position of rostrum, ca. in the level of cheliceral base. The setae cling to each other. The third pair also grows from lateral bulks. This pair is the longest, each seta ca. 80 μm long, slightly serrate. The fourth pair of signficant setae does not has its base laterally, but more shifted to dorsum. These setae are straight, also slightly serrate and ca. 50 μm long. Sensilla are slender, long (60 μm), clavate-capitate and rough. Tibia I and tibia II with solenidia, tarsi monodactyle. Femora not noticeably enlarged.

Discussion. This mite belongs to suborder Brachypylina (Oribatida) based on the following combination of characters after Walter (2006): Solenidia erect on distal leg segments, tarsi with one claw, pteromorphs present, adults beetle-like with prodorsal trichobothriae, body articulation holoid, imagines with 4 pairs of legs, adults with prodorsal trichobothriae, 1 pair of clavate (capitate) sensilla, capitulum withdrawn into head or camerosome.
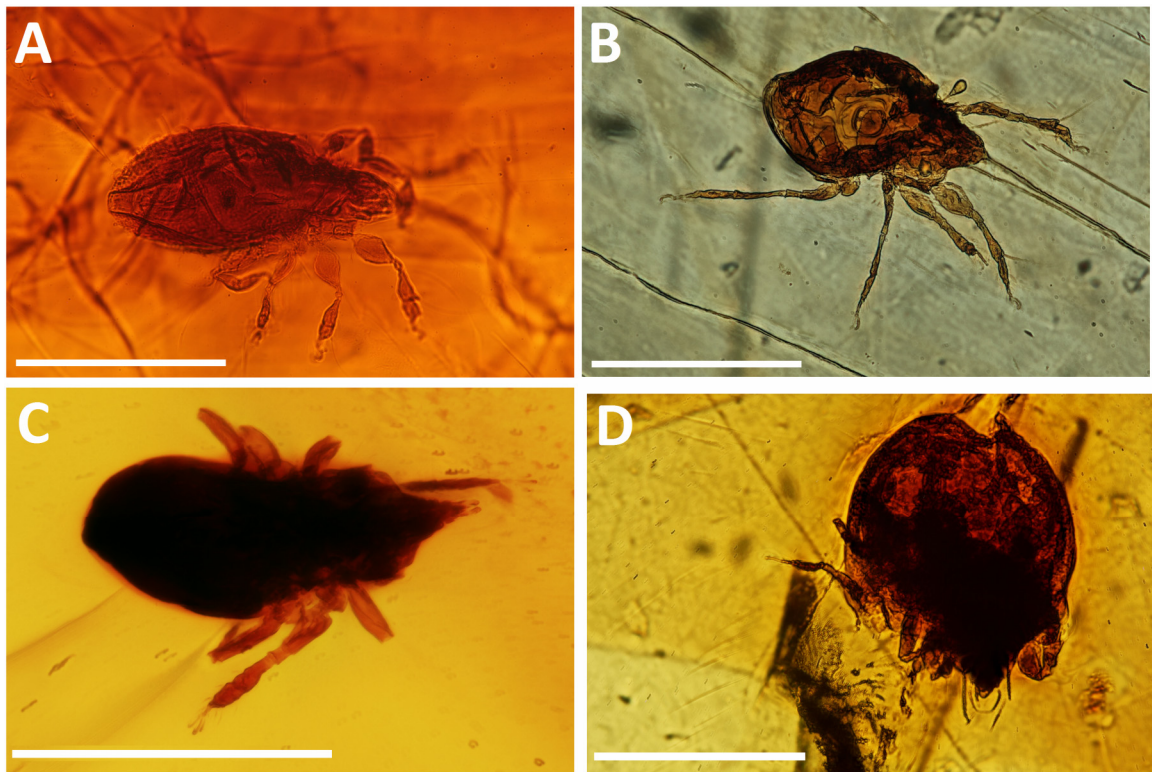
Fig. 15. – Oribatid mites (Brachypilina) in Študlov amber. **A**, no. 94. **B**, no. 227. **C**, no. 232. **D**, no. 103. Scale bars: 200 μm

Summary: Oribatida in amber from Študlov

All inclusions of mites from Študlov amber belong to Oribatida, at least three of them (but probably all) can be determined as members of Brachypylina. Both taxa share some morphological characteristics with Prostigmata, but the sum of characters shows clear divisions. All four specimens are well sclerotised and thus considered as adult.

Oribatida in general are numerous ubiquitous decompositors of organic matter, feeding on fungi, algae or plants. Their size varies from 150 μm up to 1.5 cm and can be easily found in temperate forests (Behan-Pelletier & Winchester 1998). Three of four Študlov mites are tridactyle. Tridactyly is supposed to be adaptive trait for arboreal species, which inhabit tree canopy. Monodactyly, on the other side, is more often found within soil species. Species living on trunks usually have three claws as well as canopy species (Karasawa & Hijii 2004). The mite specimen no. 94 was trapped together with an archipsocid barklouse, which also probably sought in the tree surfaces. It is dorsovenrally flattened, so it is possible that the species was used to live under the tree bark. Specimens nos. 94 and 227 are very similar in size and shape and could be closely

related or belong to the same species. Some of the measurements of their body parts differ, but it could have been caused by different preservation. Only the mite no. 227 has syninclusions – the previously mentioned barklouse, microscopic fungal hyphae and a fly remain. Within all four mite inclusions, the most problematic part of their body is the notogaster, which is always somehow damaged, cracked, as if the convex shape meant a disadvantage in fossilisation. Thus it is not possible to determine these mites using details on the dorsum of notogaster. The legs and gnathosoma, in contrast, have been preserved better in all cases, only with the problem that the legs are often incomplete - they broke in their narrowest point (genu) as the mite was trying to escape from fresh resin.

Brachypylina is a very old mite suborder: the oldest representative was found in Swedish lower Jurassic sediments (Sivhed & Wallwork 1978). While researching extant forest mite diversity, Brachypylina tend to be the most abundant of all mite groups (Behan-Pelletier & Winchester 1998, Mumladze et al. 2015, Wehner et al. 2016). However they might have been overlooked as fossils and their fossil record in amber is not as large as one would expect. Some of them were found in the Lower Cretaceous of Spanish amber (Arillo et al. 2009 in Sidorchuk 2018). Arillo et al. (2012) mentioned 10 brachypyline mites found in the Jurassic and Cretaceous deposits, of which the oldest amber record comes from the Albian (Spanish amber). One brachypiline mite was also found in Baltic amber together with a carabid beetle (Cai et al. 2017), but generally there are very few Cenozoic amber fossils of Brachypylina. Surprisingly, despite the fact that Brachypylina have been quite abundant in all forest microhabitats, only small amount of oribatid mites were found in amber and classified within this suborder.

Class: Insecta

Superorder: Condylognatha

Order: Thysanoptera

Family indet. (figs. 16; 19 – A).

Material. No. 219 – Syninclusion of a bug imago and thrip imago

Description. Body length 520 µm, head 90 µm long , thorax 180 µm, abdomen 250 µm. Head slightly elongated. Eyes not entirely on the front of head. Hind femur 130 µm long, tibia 90 µm. Body darkly pigmented, strongly sclerotised. Two pairs of narrow membranous wings are folded over the abdomen, fore wings 515 µm long. Fore- and hind femora enlarged, ca. 50 µm wide.
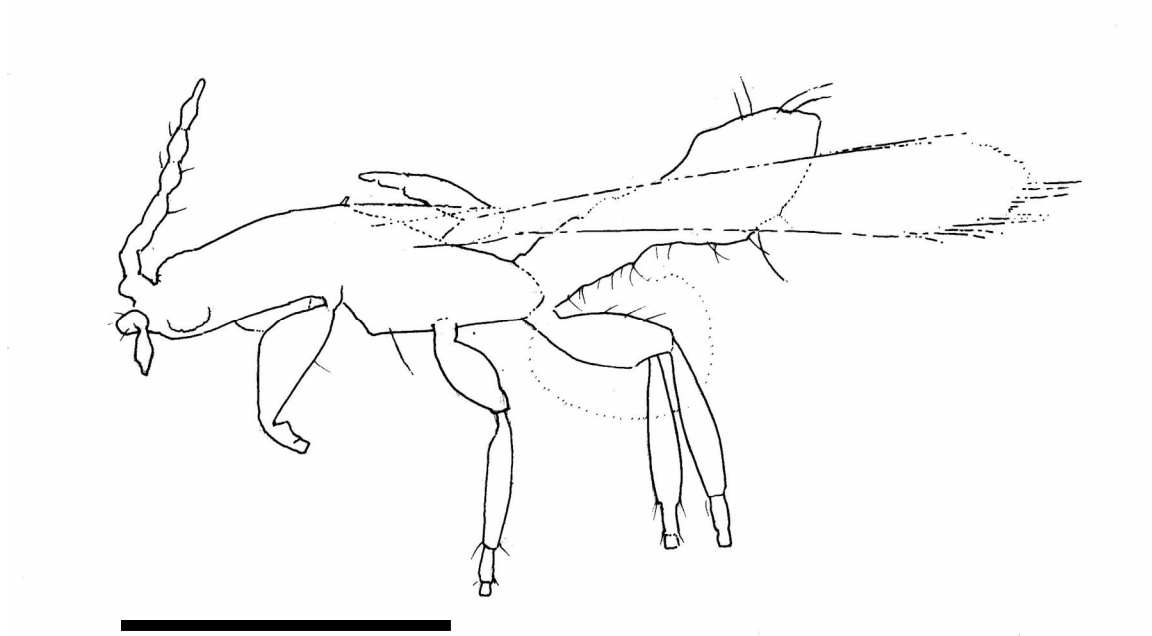
Fig. 16. – Thysanoptera, family indet., imago from no. 219, scale bar: 250 µm.

Discussion. Unfortunatelly, the present specimen is embedded together with a bug imago (Heteroptera: ?Malcidae), which makes it difficult for observation and partially hidden the crucial structures from the lateral view. Therefore, its systematic position remains uncertain.

Suborder: Terebrantia

Family: Thripidae Stevens, 1829 **(fig. 19 – B.).**

Material. No. 11 - syninclusion of a thrip imago and a non-biting midge imago in clear, transparent amber piece, impaired only by a few refractory planes, perpendicular to plane of observation.

Description. Body 510 μm long. Head rectangular, 90 μm wide, large compound eyes placed on lateral edges. Antennae 95 μm long, most probably consisted of 8 antennomeres (7 to 9 depending on considering the last flagellomere), all longer than wide, but rather moniliform than filiform. Pedicellus goblet-like. First flagellomere with narrow peduncle. Second flagellomere short, third and fourth flagellomeres large and joined together. Terminal flagellomeres narrowed to a style, ended with two equally long setae, forming a V-shape. Style ca. 4x longer than wide. Thorax about 150 μm long, pronotum not wider than head. Abdomen 265 μm long, posterior sections of dorsal split seems to be separated from each other. Macropterous, wings narrow and covered by long fringe cilia. Only one (metathoracal) leg is stretched to expose relatively wide femur, other legs clutched together under the body.

Discussion. Middle part of the body seems clutched and probably also collapsed, which means that both thorax and abdomen could have been basally broader than they appear. Antennae are the most significant of body parts, allowing determination of this fossil more precisely. The overall antennal pattern shows no suspicious values or shapes, it is consistent with the leaf-feeding family Thripidae (see Zhang et al. 2019 for figures). Terminal part of each antenna hardly discerinble, so it can not be resolved, if there are 7 (like *Scirtothrips* Shull, 1909), 8 or 9 (like *Anaphothrips* Uzel, 1985) antennomeres, and if the fusion is only the result of fossilization. The antennal pattern can be called "thripoid". Further characters found on this specimen, corresponding with family Thripidae after Bhatti (2006): base of abdomen not sharply constricted, broadly joined to metathorax; fore wings lacking callosities and saccate projections, wings narrow, slender, without reticulations, covered with hair-like microtrichia; fore femur and tibia together much longer than pronotum, legs without annular rows of microtrichia on femora and tibiae; terminal flagellomere with two setae arising just before the apex.

Confirmation of presence or absence of furcal sensoria on antennomeres III and IV would be necessary for further determination, as well as better preseravtion of abdomen (abdominal rows of setae) and wings.

Thripidae is a large family with over 2000 species (Zhang et al. 2019). Thrips generally have been quite commonly found in amber deposits. For instance, in Rovno amber, there are 76 thrips recorded, of which 49 % (37 thrips) are specimens of the dominant genus *Praedendrothrips avus* Priesner, 1924 (Thripidae). Except of this species, there are another six genera and five families identified, but so far no other Thripidae have been found (Shmakov & Perkovsky 2009).

The *Praedendrothrips avus* is surprisingly rare in Baltic amber (Shmakov & Perkovsky 2009). Schliephake (1999) described 22 species of thrips from Baltic and Bitterfeld amber, unfortunately he did not distinguish differences between these two fossil deposits, so it is not obvious whether the described speciec comes from the Baltic or the Bitterfeld deposit. He mentioned at least 7 species of the family Thripidae and some other with poor preservation. In French Oise amber, several Thripidae have been mentioned (Brasero et al. 2009) and described by Nel et al. (pers. comm. - in prep.), including for example genera *Synaptothrips* Trybom, 1910*, Stenothrips* Bhatti & Mound, 1980*, Thrips* Linnaeus, 1758*,* or *Oxythrips* Uzel, 1895.

An overview of thrips of Rovno, Baltic and Bitterfeld ambers are available (Shmakov & Perkovsky 2009: Table 1). It seems that for Baltic amber, genera like *Taeniothrips* Trybom, 1910 or *Protoxythrips* Priesner, 1929 are more common. According to this table, Bitterfeld amber differs from Baltic by occurrence of completely different species (not genera) and the Rovno amber differes from both of them, because *Praedendrothrips avus* is the only representative of Thripidae found in the Ukrainian deposit. Thripidae are not exclusively recorded in Cenozoic deposits; the genus *Tethysthrips* was described from Early Cretaceous of Lebanese amber (Nel et al. 2010).

Order: Hemiptera

Suborder: Sternorrhyncha

Superfamily: Coccoidea

Family: Eriococcidae Afifi & Kosztarab, 1967

Genus et species indet. (fig. 19 – C).

Material. No. 18 – scale insect larva in transparent amber piece without syninclusions.

Description. Total body length 380 μm, maximum width 205 μm (thorax). Body oval, dorsoventrally flattened. Head opisthognathous, dorsally covered by the pronotum. Antennae 115 μm long, consisting of at least 8 antennomeres, sparsely bearing setae. Legs relatively long, jutting out of the body silhouette, fore femora 50 μm, middle femora 65 μm, hind femora 55 μm, fore tibiae 65 μm, middle tibiae 70 μm, hind tibiae 55 μm, tarsi not clearly discernible. Pygidium with two posterior anal lobes, each bearing one macroseta, ca. 105 μm long. Anal lobes 30 μm long and about 20 μm wide. Several distict setae appear all over the body from dorsal and lateral sides.

Discussion. This specimen belongs to Eriococcidae due to the following combination of characters after the key given by Miller et al. (2014): more than 6 antennomeres, legs present, fore legs equal to (or slightly smaller) than other legs, tarsus shape straight, anal lobes large and protruding, enlarged setae on projecting anal lobes present. It is also clear that this felt scale is not an adult male, which would be alate and not with reduced body structures (Cook et al. 2000). After the body parts proportions it is probably a larva (Szita, pers. comm.), but we cannot definitevely exclude an adult female due to taphonomy.

However, Eriococcidae do not seem to be a monophyletic family. Cox & Williams (1986) found no autapomorphy and considered Eriococcidae as paraphyletic. In this family, gall-inducing habits have been known, but clearly evolved multiple times (Cook & Gullan 2004). Cook et al. (2002) published a phylogenetic analysis based on nuclear small-subunit ribosomal DNA, in which Eriococcidae would form a paraphyletic taxon, including Dactylopiidae, Asterolecaniidae, Beesoniidae and Stictococcidae.

Eriococcidae imagines bear various shapes and forms (as shown in Cook & Gullan 2004). Long setae on anal lobes have been found on the first nymph instars of various eriococcids, such as *Opisthoscelis* Signoret, 1869b, *Tanyscelis* Hardy & Gullan, 2010 (Hardy & Gullan 2010) or *Madarococcus* Hoy, 1962 (Hardy et al. 2008), but sometimes persist into female adulthood, as shown on *Montanococcus thriaticus* Hendreson, 2007 (Henderson 2007) or *Acanthococcus riojensis* Juaréz & González, 2017 (González et al. 2017). We can find very similar anal lobes on our specimen no. 18 tentatively attributed to the genus *Eriococcus* Maskell, 1893 (Hardy & Gullan 2007). It should be mentioned

that genus *Acanthococcus* and *Eriococcus* are most often synonymised (Miller & Gimpel 1999), but simultaneously treated different by various authors.

Males of Eriococcidae represented by *Kuenowicoccus pietrzeniukue* Koteja, 1988 and *Cancerococcus apterus* Koteja, 1988 are known from the Baltic amber (Koteja 1988). The same author also described five new species of Eriococcidae from Baltic amber in stage of 1st larval instar "crawlers" and had trouble in comparison with the recent species (Koteja 1988). Fossil scale insects are found rather scarsely in ambers. Koteja & Azar (2008) investigated 30 specimens of 7 scale insect famillies (mostly males) from the Lower Cretaceous amber of Lebanon and some of them were probably belonging to Eriococcidae. Koteja (2004) described 17 specimens of scale insects (mostly males) from the mid Cretaceous amber of Myanmar, but no certain evidence of Eriococcidae was found yed.

Superorder: Psocodea

Order: Psocoptera

Suborder: Psocomorpha

Family: Archipsocidae Enderlein, 1903

?*Archipsocus* Hagen, 1882 (figs. 17; 18; 19 – E).

Material. No. 94 – Syninclusion of a female barklouse with a moss mite, an incomplete fly and fungal hyphae of at least 2 types in layered amber piece with high transparency and tenacity. The four inclusions are not in direct contact. Most of the fossilised body of the barklouse is well preserved, however small dorsal region probably degradated before being overlapped by new resin layer.

Description. Body 1.15 mm long (head to tip of abdomen). Head hypognathous, 400 μm wide. Eyes prominent, even substylate, placed laterally. Antennae with 13 antennomeres, scape and pedicel about similar size, ca. 60 μm long. First flagellomere (F1) markedly elongated - 130 μm long. F2-F6 about half length of F1. F7-F10 only a little shorter than F2-F6. Basally, all antennomeres covered with setae. Maxillary palpi four-segmented with well discernible enlarged last palpomere 92 μm long. Pronotum bulged, strongly convex, covered with long setae. The specimen is macropterous. Forewings 1.3 mm long, hyaline with strongly reduced venation, only costal area thickened up to slightly more than 1/2 of the fore wing length, then costal margin regular. Other veins on

forewing not discernible with exception of evanescent ScP. Wing membrane densely and homogeneously covered by 30-50 µm long setae. Hindwings about 1.15 mm long. Legs almost homonomous, all with 2 tarsomeres. All femora ca. 270 µm long. Fore tibiae 300 µm long, mid tibiae 300 µm long, hind tibiae 410 µm long. Abdomen 550 µm long, with two external valves of gonapophysis.
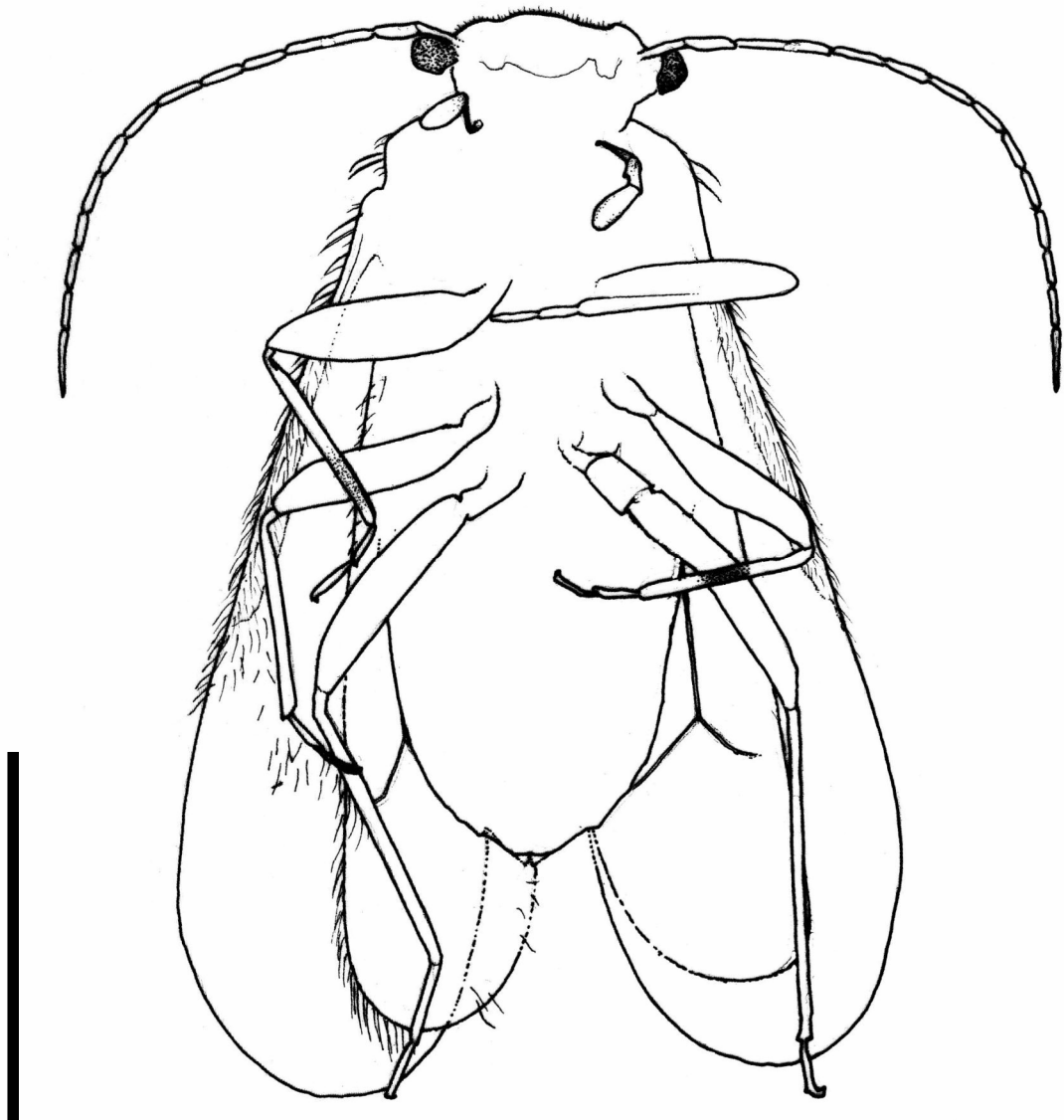
Fig. 17. – *?Archipsocus* sp. (Archipsocidae) from no. 94, scale bar: 500 µm.
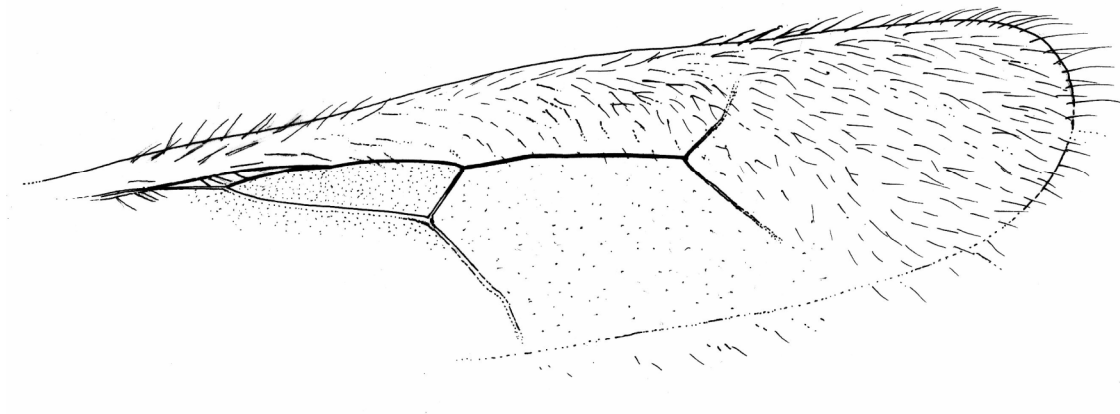
Fig. 18. – Wing of the *?Archipsocus* sp. (Archipsocidae) from no. 94.

Discussion. Following the keys to the families of Psocoptera of Smithers (1990) and morphology of Psocomorpha by Yoshizawa (2005), this fossil barklouse is determined as a member of family Archipsocidae. It is the most basal clade of Psocomorpha (Johnson & Mockford 2003). The main diagnostic characters can be found in strongly reduced venation of forewing densely covered by setae, and especially the pattern of hindwing venation. The bulged pronotum is another significant character found in Archipsocidae (Yoshizawa 2005), not so common in other families of Psocomorpha. The hind wing venation pattern resembles the one in *Archipsocus puber* Hagen, 1882 described from the lowermost Eocene amber of Oise (Nel et al. 2005). The closed elongate basal cell excludes genus *Pararchipsocus* Badonnel, Mockford & Garcia Aldrete, 1984 and *Pseudarchipsocus* Mockford, 1974 (Smithers 1990). Due to its macroptery and presence of subtriangular external gonapophysis it is most probably a female attributable to genus *Archipsocus* Hagen, 1882. The closely related genus *Archipsocopsis* Baddonel, 1966, which is viviparous, has reduced gonapophysis (Smithers 1990) and there have been no confirmed fossils of *Archipsocopsis* from amber deposits.

The family Archipsocidae has been known from the Eocene strata, such as Baltic amber (Weitschat & Wichard 2010) and Rovno amber (Engel & Perkovsky 2006). Similarly, diverse collection of fossil Psocoptera comes from Oise in France, where Archipsocidae are represented also by *A. puber* (Nel et al. 2005). Archipsocidae are also

known from Oligocene/Miocene amber of Chiapas in Mexico (Mockford 1969). Despite Archipsocidae are considered basal family of Psocomorpha, there have been no Cretaceous representatives of Archipsocidae so far.

A male, brachypterous barklouse specimen was also found in Študlov amber in sample no. 260 (see **fig. 19 – D**), showing too few features to be determined.

> **Fig**. **19.** – Thysanoptera and hemiptera from Študlov amber. **A**, Thysanoptera (family indet.) and Heteroptera (family indet.) from no. 219, scale bar: 500 μm. **B**, Thripidae (Thysanoptera), (genus et species indet.) from no. 11, scale bar: 250 μm. **C,** scale insect (Eriococcidae) (genus et species indet.) from no. 18, scale bar: 200 μm. **D,** Psocoptera (family indet.) from no. 260, scale bar: 1 mm. **E,** *?Archipsocus* sp. (Archipsocidae) from no. 94 scale bar: 500 μm.
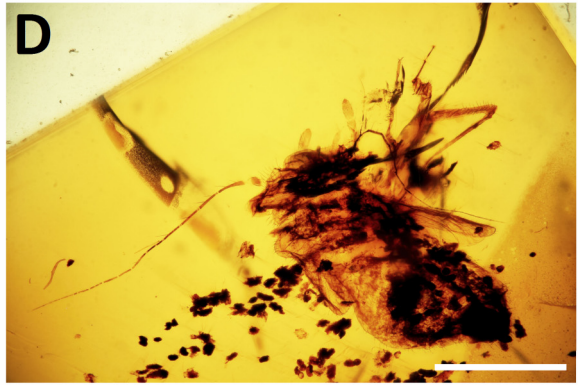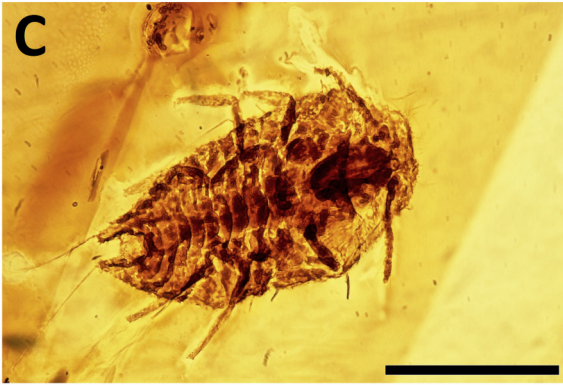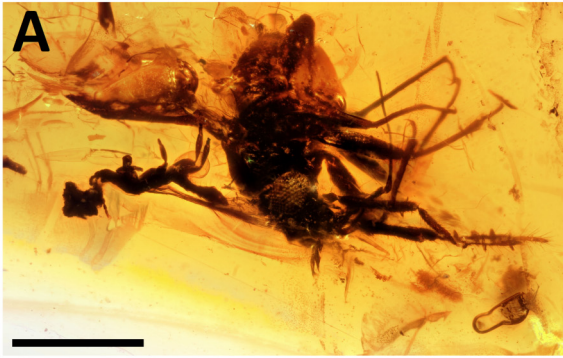
Endopterygota

Order: Hymenoptera

Along the newly discovered fossil hymenopterans, it is necessary to note a scelionid wasp as *Moravoscelio bednarikii* Nel & Prokop, 2005 previously described from Študlov amber (Nel & Prokop 2005). Further minute wasps of the families Chalcididae Latreille, 1817 and Scelionidae Haliday, 1839 have been found in few samples of Študlov amber (see appendix). So far none of them could have been attributed neither to *Moravoscelio*, nor to any other known genera, because the preservation of these specimens is not sufficient.

Suborder: Apocrita
Superfamily: Chalcidoidea
Family: Pteromalidae Dalman, 1820
Subfamily: Pireninae Haliday, 1844
Genus et species indet. (figs. 21 – A; B)
Material. No. 12-A (1) - Formerly a large amber piece containing 7 syninclusions, later broken into the three fragments during preparation: A female of chalcid wasp [12-A(1)], three scelionid wasps, two flies (Diptera) and fragments of insect legs.

Description. Body well sclerotised, 1.15 mm long, all body parts well preserved. Head 210 μm long, 325 μm wide. Antennae clavate, consisting of at least 9 antennomeres: enlarged scape + pedicel connected to scape, together with flagellum bent beside scape. Flagellum with traces of annulation, clavate. First flagellomere almost indiscernible, followed by five similar in size, flagellomeres annulate. Flagellum length 190 μm, last recognizable flagellomere 90 μm long and 55 μm wide. In fact the last visible flagellomere consisted of three secondarily multijointed, clava itself and other two flagellomeres to the final number, however in this case there is no trace of the last secondarily multijointed flagellomere. Legs covered with short setae. Profemora 240 μm long. Fore and metatibiae bare, but mesotibia bearing a single setose spur. Coxae large, sclerotised. Tarsi with prominent arolium and a pair of slender claws. Tarsal formula 5-5-5. Forewings with pattern of pteromalid reduced venation: submarginal, marginal, stigmatal and postmarginal veins present, as well as small stigma and short hairs on the

wing membrane. Hindwings present, short as well as forewings, bearing a row of setae along posterior wing margin, distinctly longer than setae on the wing membrane. Abdomen with a short ovipositor..

Discussion. The following combination of characters compared to the key after Gibson et al. (1977) supports the assignement of this fossil into family Pteromalidae: fully winged; metafemur not enlarged, longer than wide; tarsi 5-segmented; forewing stigmal vein arising at obtuse angle from marginal vein; flagellum with 3-6 clearly visible segments. Further traits, typical of Pireninae according to Gibson et al. (1997) are as following: antennae with fewer than 7 discernible segments between pedicel and clava; metacoxa without very dense setae; antennal flagellum with second funicular anellus not much smaller than first or third segment; forewing basally with bare areas. Within Pireninae, there is a trend of anelli reduction, so that the anelli are barely distinguishable (Mitroiu 2016), which is also the case of this specimen from Študlov.

Pteromalid wasps exhibit a variety of parasitoid strategies. Of them, Pireninae a smaller subfamily counting more than 10 genera, often attacking gall midges (Cecidomyiidae) and other flies (Graham 1969). Curiously, the same specimen (no. 12) includes a female of biting midge of the genus *Leptoconops* (see below) and in another sample (no. 221), a gall midge of subfamily Lestremiinae (Cecidomyiidae) was also identified. So this parasitoid wasp surely had sufficient number of potential hosts.

Unfortunately, only few representatives of Pireninae are known from fossil record. There is at least one specimen from Oise amber (France), which was examined by synchrotron X-Ray microtomography showing the remains of internal structures like muscular tissue and brain (Van de Kamp et al. 2014).

Infraorder: Aculeata
Family: Formicidae Latreille, 1809
Subfamily: Myrmicinae Lepeletier de Saint-Fargeau, 1835
Genus et species indet.
Material. No. 9 - Imago of an ant in transparent amber piece without syninclusions. The body lies inside of a hazy coating, which makes it difficult to distinguish between some other body parts. Part of head is missing anteriorly, as well as most of the abdomen.

Rudiments of legs clumped on the margins of the sample, one metathoracic leg complete.

Description. The whole body could have been about 4 mm long. Antennae 2.5 mm long, composed of 11 or 12 antennomeres. Scape elongated, but the antennae do not seem to be elbow-bent, instead the few terminal flagellomeres are curved upwards. The slightly convex thorax with a short propodeal spine visible from lateral view. The metathoracic leg protruding, femur >1 mm long, tibia 1.1 mm long, tarsus with five tarsomeres, first tarsomere 800 μm long, second tarsomere 400 μm long, subsequent tarsomeres clearly shortening. A stout, single apical tibial spur present on metatibia. Petiole humpy, followed by slender postpetiole. The postpetiole is not bulged and it is slightly narrowing before rest of abdomen.

Discussion. Despite rather poor preservation of this fossil, some significant characters can be discerned, pointing to its classification as a member of Myrmicine. Antennae with 11 or 12 antennomeres typical for female workers of Myrmicine as noted by Wheeler (1922), and especially, the petiole which is followed by postpetiole (Collingwood 1979). Except the presence of postpetiole, it is very difficult to find other shared characters within the specimen from Študlov and the rest of Myrmicinae. The metatibial spur is simple or absent within Myrmicinae (Collingwood 1979). The narrow postpetiole is not very common amongst myrmicines, resembling e. g. the recent species *Recurvidris lekakuli* Jaitrong et al., 2019, or the Miocene *Pheidole anticua* Casadei-Ferreira, Chaul & Feitosa, 2019 described from the Dominican amber.

Myrmicinae ants sporadically appear in Cenozoic ambers. Radchenko & Dlussky (2017) described new species of an extinct genus *Stigmomyrmex* Mayr, 1868c from Baltic and Bitterfeld ambers. *Eocenomyrma* Dlussky & Radchenko, 2006 is an extinct genus known from the Baltic amber, represented by the recently described *E. groehni* Radchenko, 2020 (Radchenko 2020). The Rovno deposit does not drop behind. One nicely preserved worker of the genus *Monomorium* Mayr, 1855 was identified by Radchenko & Perkovsky (2009), and later other worker of genus *Vollenhovia* Mayr, 1865 was described from the same locality (Radchenko & Dlussky 2013). Radchenko & Perkovsky (2016) discussed about the origin of Myrmicinae and estimated its age to

early Cenozoic. So far, no evidence of Myrmicine from the Cretaceous has been reported.

Suborder: Apocrita

Incertae sedis

Family: Stigmaphronidae Kozlov, 1975

Tagsmiphron **sp.** Engel & Grimaldi, 2009 **(figs. 20; 21 – C).**

Material No. 263 - Prepared slide of a well preserved stigmaphronid wasp, female imago. Body partly hidden by small air bubbles.

Description. Body ca. 1 mm long, head 200 μm long, 250 μm wide. Middle ocellus apparent, compound eyes large. Antennae ca. 500 μm long, 11-segmented, bases of scapi close from each other. Scapus elongated, 110 μm long. Pedicel and last flagellomere of similar size. Pedicel triangular, cone-shaped, widening from base to the top. First flagellomere smallest and shortest. All flagellomeres except the last one rectangular from lateral view; cylindrical. Last flagellomere cone-like, but widest at base. Antennomeres not fused. Head slightly rotated. Mesosoma ca. 300 μm long, dorsally strongly sclerotised, mesoscutellum foming a shuttle spit. All coxae enlarged. Front legs shortest, subtle and narrow, with single tibial spur. Mid femora slightly enlarged, tibiae with two spurs. Hind coxae and femora strongly enlarged. Femora ca. 220 μm long and up to 120 μm wide. Hind tibiae large, 170 μm long, triangular, widening to the top, bearing two spurs. Marginal spurs large, almost as long as tibia. The spur arising from the middle of tibial posterior enlarged end is clearly shorter. Tarsal formula 5-5-5. Wings folded on dorsum. Abdomen with short ovipositor. Ventral abdominal structures partly broken off. The whole body seems to conserve some inner tissues, like brain or muscles connected to ovipositor.
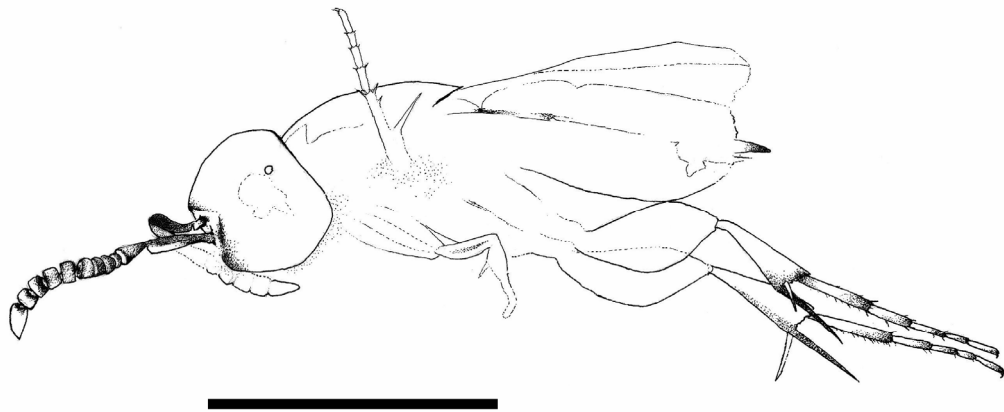
Fig. 20. – *Tagsmiphron* sp. (Stigmaphronidae) from no. 263, scale bar: 500 μm.

Discussion. This wasp represents a rare evidence of Eocene Stigmaphronidae family. All Stigmaphronidae seem to share certain characters, like size size (0.7 to 2mm) (Engel & Grimaldi 2009, Ortega-Blanco et al. 2011), shuttle-shaped margin of mesoscutellum (see figures in Engel & Grimaldi 2009), typically 11-segmented antennae (McKellar & Engel 2011) or Ortega-Blanco et al. (2011) or tibial-spur formula 2(1)-2-2 (Engel & Grimaldi 2009). Engel & Grimaldi (2009) provided a key to the family Stigmaphronidae. Following this key, our fossil could be determined as a member of genus *Tagsmiphron*, judged by these characters: metatibial spurs stout, forewings with Rs present, preoccipital area not ridged immediately anterior to sharply angled posterior border of head, distal margin of metatibia without spicules, funicular articles of antennae not compact, width greater than length, forewing Rs well developed, protibia with single spur. In this key, authors used as one of the significant character the metatibial comb of 5-7 spicules, present within genus *Burmaphron* Engel & Grimaldi, 2009, however in the figure that should illustrate metatibial comb, the comb is placed on metafemora. *Tagsmiphron* is supposed to be a more derived genus form of stigmaphronids (Ortega-Blanco et al. (2011), so it is possible that it could persisted to the Eocene. However, this only stigmaphronid wasp known from the Cenozoic so far.

Until now, Stigmaphronidae were known from the Cretaceous strata only. A complex review of Stigmaphronidae with characteristics of the genera from the Cretaceous ambers of Spain, Lebanon, New Jersey, Alaska, Siberia, Myanmar, Canada, and also the compression fossils of Siberia and Mongolia can be found in Ortega-Blanco et al. (2011) . Surprisingly, ca. 50 stigmaphronids from 23 species have been discovered

in Albian Spanish amber (Álava), so this family had to be quite wide-spread during the Cretaceous or its certain stages.

Systematically, the stigmaphronids were considered as a group of Ceraphronoidea and were supposed to be parasitoids of various insects (Engel & Grimaldi 2009, Ortega-Blanco et al. 2011), but Mikó et al. (2018) demonstrated some significant differences between stigmaphronids and the rest of Ceraphronoidea, while there has been only limited amount of common characters (like two protibial spurs). However, these authors are uncertain with the systematic placement, so they leave stigmaphronids as *incertae sedis*, possibly as an inner group of Aculeata.

This fossil of stigmaphronid female wasp is the first known evidence of this family in Cenozoic (Eocene), and thus, the last survivor representative of this family.
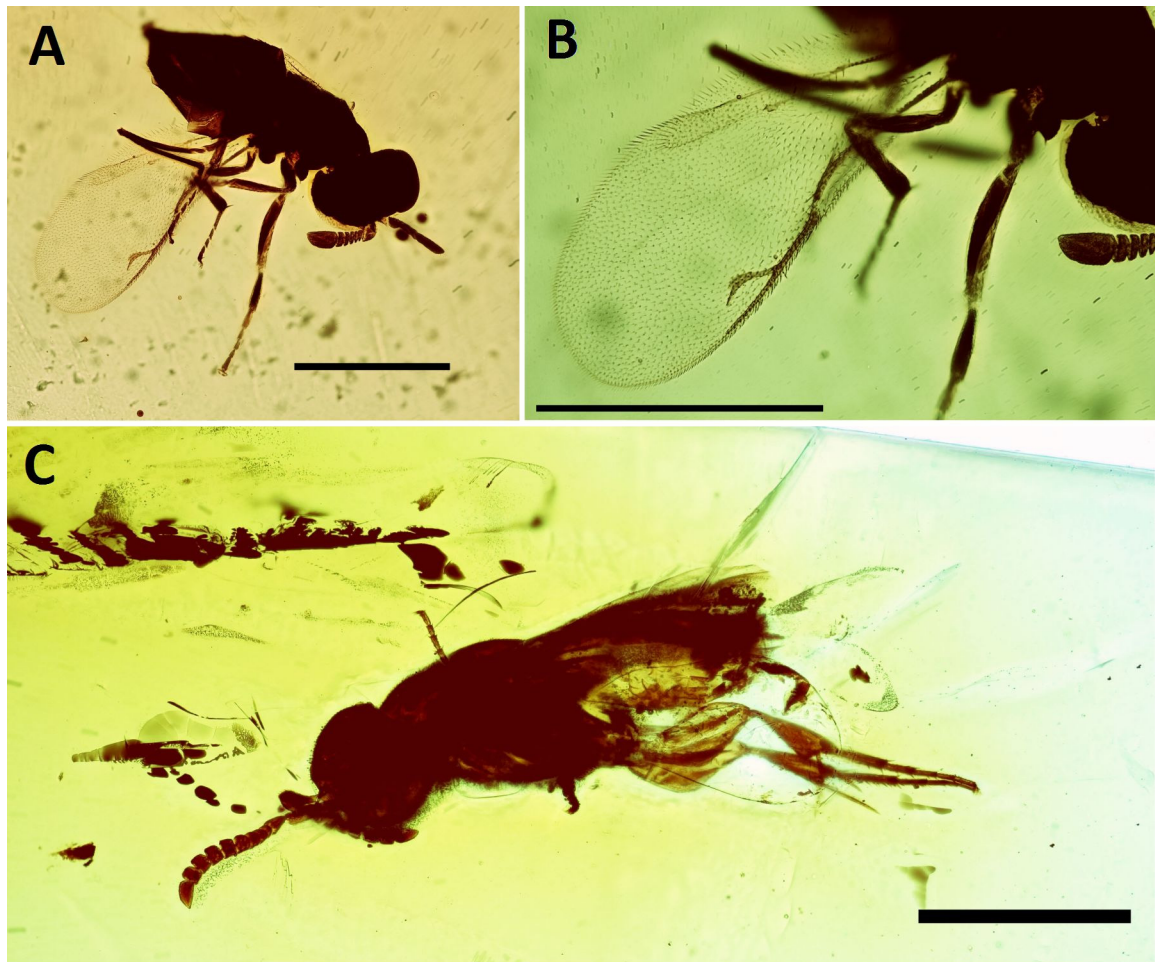
Fig. 21. - Hymenoptera of Študlov amber. **A,** Pireninae (genus et species indet.) (Pteromalidae) from specimen no. 12-A, scale bar: 500 µm. **B,** the same as A, wing detail, scale bar 500 µm. **C,** *Tagsmiphron* sp. (Stigmaphronidae) from no. 263, scale bar: 400 µm.

Order: Coleoptera

Family: Latridiidae Erichson,1842

Subfamily: Corticariinae Erichson, 1842

genus et species indet. (figs. 22; 23 - B; C)

Material. No. 1 – Syninclusion of an imago of a minute brown scavenger beetle, an incomplete insect body and a stellate plant hair.

Despription. Body 0.85 mm long and 0.33 mm wide. Head hypognathous, widely oval from above, 85 µm long and 190 µm wide. Eyes developed, located laterally, but not protruding. Antennae consist of 11 antennomeres, both scape and pedicel enlarged and elongated. Scape is the most pigmented of all antennomeres, 2.4x longer than wide, club-shaped. Pedicel base is attached to scape in angle of 45°, the whole shape of the pedicel is also club-like, but curved. It is also less sclerotised than scape. The first five flagellomeres not elongated and rather square-shaped. Last four flagellomeres form a club 95 µm long and 30 µm wide, enlarged gradually and more pigmented as well. Antennae pubescent, each antennomere bearing setae. The largest terminal antennomere bears setae of two sizes (ca. 45 µm and ca. 20 µm long). Prothorax roughly oval, 145 µm long and 210 µm wide, laterally coarse or even thorny on its edge, with pointed protuberances, gently pubescent. Scutellum not apparent. Elytra not fused, covering almost the whole abdomen, terminated with round margin before the last ventrite. Elytra widen promptly at basis (300 µm), but they are widest on the level of first ventrite (330 µm). Hindwings present, membrane hyaline, part of costal and posterior margin protrudes from under the elytra. Apex without discernible venation, but it is densely covered by microtrichia and along the wing apex and posterior margin with long macrosetae, about 55 µm long. Five ventrites are discernible, Tarsal formula not clerly visible, 3-?-3.
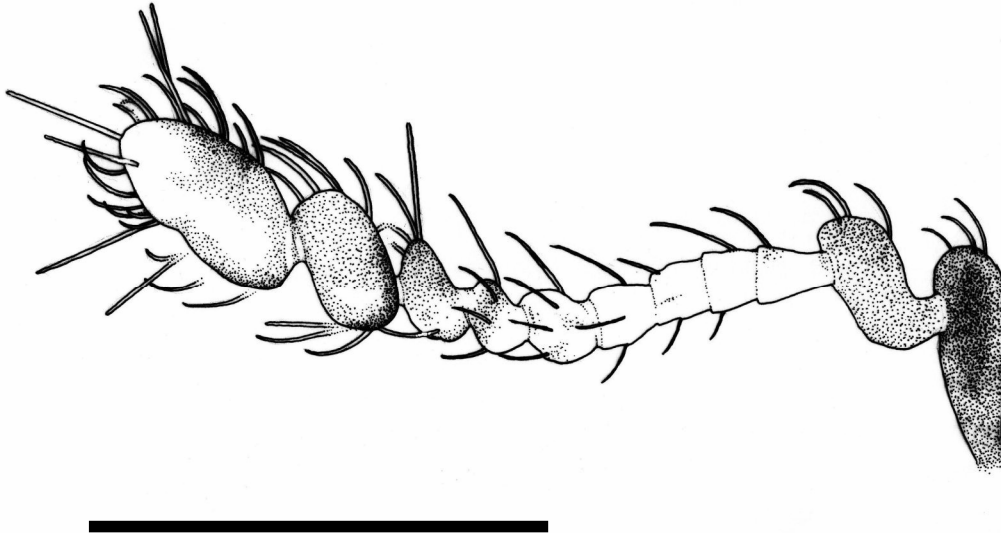
Fig. 22. – Corticariinae (genus et species indet.) (Latridiidae) from specimen no. 1, scale bar: 100 μm.

Discussion. This fossil beetle belongs to mycophagous family Latridiidae, after characteristics of this family by Hartley & McHugh (2010) and Lord et al. (2010): small size (about 1 mm), the overall body shape, tarsal formula 3-?-3, elytra covering almost whole abdomen, clavate antennae with enlarged scape and pedicel and 11 antennomeres, small or reduced scutellum, elytra surface not smooth. Length of the fossil beetle, which is practically <1 mm, can be suspicious, but there are records of such small fossil Latridiidae, as *Dienerella nielseni* Reike, 2012, which is 0.91 mm long (Reike 2012). The family Latridiidae has not been well defined by morphological characteristics, however there are two morphologically slightly different subfamilies. Hypognathous head and pubescent, compact body allow assignment of this fossil to subfamily Corticariinae (Hartley & McHugh 2010). In Corticariinae, most species have normally developed eyes and there are both macropterous and brachypterous/apterous species (Trikhleb 2009). This fossil specimen has distinctly basally broad elytra. The visible part of wing membrane does not show many characters with exception of long macrosetae along the wing apex that matches with members of Latridiidae (Trikhleb 2009). Round prothorax with tiny spines on its edge can be found in Corticariinae (for example Otero & Lopéz 2009), while Latridiinae Erichson, 1842 usually have angular, elongated prothorax (e.g. Reike et al. 2013).

The vast majority of fossil Latridiidae come from the Baltic amber, with examples of both subfamilies Latridiinae and Corticariinae subfamilies (Reike et al. 2013, Reike 2012). Reike et al. (2013) recently described *Dieneremia rueckeri* (Latridiinae), and except of this species description, other detailed records are quite rare. In specimen no. 1, as within many other fossil Latridiidae, male genitalia would be necessary to determine genus or species. Reike et al (2017) used phase-contrast synchrotron microtomography to virtually disect genitalia of their newly described species *Corticaria amberica* Reike et al., 2017, and this seems probably the only way how to reliably determine some fossil minute brown scavenger beetles. Latridiidae have also been reported from the Rovno amber, represented by *Latridius usovae* Sergi & Perkovsky, 2014 (Latridiinae) (Sergi & Perkovsky 2014). In contrast, the Cretaceous record of Latridiidae, respectively Cotricariinae, is scarce with the oldest known member known from the Late Cretaceous of Taimyr amber (Reike et al. 2017).

Order: Lepidoptera
Family indet. (fig. 23 – A)

Material. No. 233 - Syninclusion of an incomplete fly with a layer containing butterfly wing scales

Description. Scales vary in length from 50 μm to 150 μm and width up to 30 μm. Shorter ones plain and oval, longer ones rather triangular and often three-spiked on distal edge. All scales together with a few filamentous sensilla lie on a surface between two resin layers.

Discussion. These fossilised butterfly scales are the only evidence of Lepidoptera in Študlov amber. Scales are typical for butterflies, as they cover their body parts, mostly wings. They are also responsible for reflective colours of imagines, structural or pigment-based. These fossil scales persumably come from a lepidopteran wing. According to Simonsen & Kristensen (2003), butterfly wing scales from different species reach lengths between 40 μm and 500 μm, and there is a positive correlation between wing length and scale length.

Amber fossil butterflies have not been so rare, including a Miocene riodinid caterpillar (Devries & Poinar 1997), a couple of pygmy moths from Baltic amber

(Fischer 2013), or Oligocene/Miocene torticid imago (Poinar & Brown 1993). Cretaceous amber Lepidoptera are represented by three species of genus *Sabatinca* Walker, 1863 (Zhang et al. 2017). These well preserved butterfly fossils show that several morphological types of wing scales had already existed in the mid Cretaceous of Myanmar amber's origin. Single scales have also been found in the Lower Cretaceous Lebanese amber (Whalley 1986). Even older lepidopteran scales have been found in Jurassic deposits as compressions (Zhang et al. 2018).
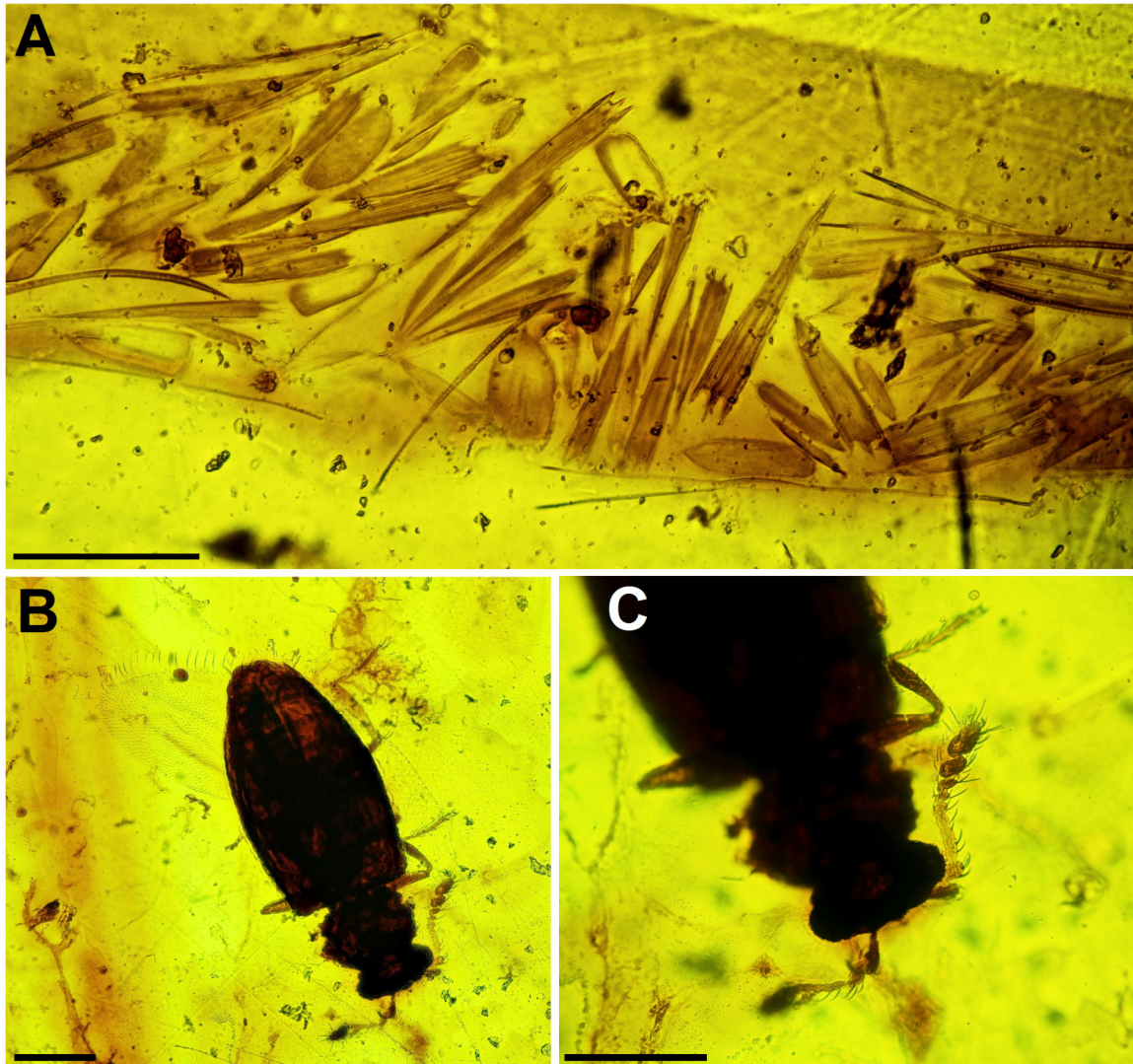
Fig. 23. - Lepidoptera and Coleoptera from Študlov amber. **A**, lepidopteran wing scales from no. 233, scale bar: 50 µm. **B+C**, Corticariinae (genus et species indet.) (Latridiidae) from no. 1, scale bar: 200 µm.

Order: Diptera

Infraorder: Culicomorpha

Superfamily: Chironomoidea

Family: Ceratopogonidae Newman

Leptoconops Skuse, 1889

Leptoconops **sp. (fig. 54).**

Material. No. 12-C – Imago of a female biting midge. Formerly large compact amber piece, later split into three fragments, containing 7 syninclusions: A female of chalcid wasp [12-A(1)], three scelionid wasps, two flies (Diptera) and isolated insect legs. Fragment 12-C is the smallest of them and contains only single fossil. Thanks to its preservation between the resin layers it can be clearly observed from its ventral and lateral sides.

Description. Body 1.2 mm long, head and prothorax well sclerotised. Head 190 μm long. Frons collapsed. Antennae 14-segmented. Scape enlarged, ca. globular, 60 μm long. Pedicel normal or just little larger than following flagellomeres. Each flagellomere ca. 30 μm long and equally wide, moniliform, seem to be flattened, but this can easily be an artifact of fossilisation. Each of them bearing at least one visible seta. Last two flagellomeres elongated, each twice as long as F10. Terminal flagellomere with terminal seta and a few additional setae. Mouthparts piercing and sucking, proboscis 190 μm long. Palps clavate, protruding from proboscis, 90 μm long and composed of 4 segments, of which the third is the largest, bearing the small fourth segment. Thorax with strongly sclerotised pronotum, anteriorly arched. A metathoracal posterior hump with a pair of setae. Halteres 165 μm long. Wing structure partly preserved, but most of veins conspicious. Abdomen ca. 840 μm long. Digestive system is darkly pigmented, originally probably filled with blood. Abdomen terminated with cerci of gently serrate surface and a few short terminal setae. Legs slender, femora unarmed, tarsi 5-segmented. Coxae large, profemora 270 μm long, protibia 250 μm long, protarsi 200 μm long. Mesofemur 310 μm long, mesotibia 280 μm long. Metafemur 300 μm long. Each tibia with single apical spur.
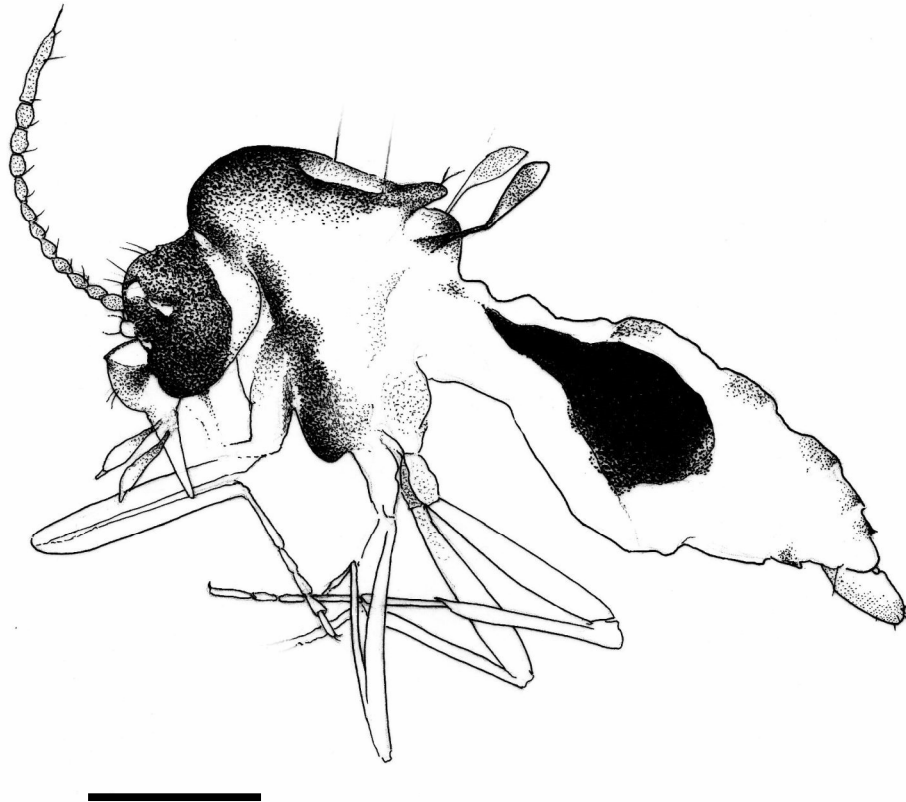
Fig. 24. –*Leptoconops* sp. (Ceratopogonidae)*, from no. 12-C, scale bar: 200 μm.

Discussion. The specimen is a female with 14-segmented antennae, which is exceptional among Ceratopogonidae. It can be assigned the the biting midge of genus *Leptoconops* Skuse, 1889, because only female *Leptoconops* can have 13 or 14 antennomeres, while other Ceratopogonidae have 15-segmented antennae (Ratanaworabhan 1971). Further characters are in agreement with attribution to this genus as noted in the key for the genera of Ceratopogonidae (Ratanaworabhan 1971): head vertex with bristles; flagellar segments subspherical or oval, each with few hairs, the terminal segment elongate; palps four-segmented; Thorax arched anteriorly; humeral pits present. Legs slender; femora unarmed; tibiae with stout apical spur. Abdomen with ninth visible segments bearing cerci. Only the hind legs do not appear the longest in contrast to the information stated in the key. The prominent cerci also seem to be quite typical for this genus.

The female has a clot of digested blood in her abdomen. Though it is impossible to determine her host, still it is an interesting finding which confirms diet in this species. Before other groups of hematophagous Diptera evolved, representatives of genus *Leptoconops* have already been feeding on blood of Mesozoic vertebrates. Genus *Leptoconops* is traditionally classified into several subgenera differing in number of antennomeres or characters on the female genitalia (see Ratanaworabhan 1971).

The oldest fossil representatives of *Leptoconops* are known from syninclusions found in the Lebanese amber, ca. 120 Ma (Borkent 2001). Two species were classified within a new subgenus *Palaeoconops* Borkent, 2001. Both species were found in several adult specimens. Another fossils attributed to this genus are known from the Spanish Álava amber (113 Ma); subgenera *Austroconops* Wirth & Lee, 1959 and *Leptoconops sensu stricto* (Szadziewski & Arillo 2003). Further findings come from 100 Million yeas old amber in France, which include synchrotron microtomographic 3D rendering of female paratype of *Leptoconops daugeroni* Choufani et al., 2011 (Choufani et al. 2011). Of course, there are also records from similarly old Burmese amber with remarkably preserved males (Szadziewski et al. 2015). In the same paper there is also an overview of *Leptoconops* fossils in amber deposits from the Lower and Upper Cretaceous and Paleogene including a map of relevant amber deposits. In Eocene ambers, the occurrence of *Leptoconops* is quite rare. A few fossils were reported by Sontag & Szadziewski (2011) from the Rovno amber, which is in this case treated by the authors as identical with species from the Baltic amber. Two females of *Leptoconops* were also found in Indian Cambay amber of Eocene age (Stebner et al. 2017).

Leptoconops is an extant tropical/subtropical genus. Adults are most active during the hottest phase of day, larvae are found in damp soil and in coastal sand with organic matter (Carter 1921 in Ratanaworabhan 1971). Temperate species described from Moscow district or Yukon territory in Canada are rather unusual (Szadziewski & Arillo 2003). The specimen from Študlov amber comes from the larger piece, which was later cut into smaller fragments.

Infraorder: Culicomorpha
Superfamily: Chironomoidea

Family: Chironomidae Newman, 1834

Genus et species indet. (figs. 25; 28 – A).

Material . No. 11 - syninclusion of a thrip imago and a non-biting midge imago in clear, transparent amber piece, impaired only by a few refractory planes, perpendicular to plane of observation.

Description. Body quite well preserved, except of the missing terminal part of abdomen, which was not included in the resin. Body length, calculated with estimated length of abdomen is ca. 0.8 mm, max. 1 mm. Head not longer than 100 μm, but as well as within some previously shown inclusions, frontal part seems to be collapsed inwards. Eyes bulging thanks to large and extremely gibbous ommatidial lenses. Antennae with seven antennomeres. Scape hidden under globular pedicel, followed by five flagellomeres. Pedicel 30 μm long. First flagellomere (F1) 40 μm long, F2-F4 ca. 23 μm long, F5 50 μm long. Flagellomeres bearing subtle setae, most of them more than 2x longer than flagellomere length, but very thin. Ocelli probably absent. Clypeus large, but mouthparts small. Palps five-segmented, segments enlarging gradually. The first segment almost indiscernible, second segment only 10 μm long. The third 35 μm long is the thickest. The fourth is 40 μm long and the last 65 μm long, ended with a bulb-shaped extension. Structures of mouthpart covered with small subtle setae. Thorax 320 μm long, anteriorly forming a significant horn, which has a blunt doubled tip and reaches level of vertex. Legs are long, slender and practically unarmed, but with some suspicious features. Coxae all very short, max. 40 μm. They are all equipped with several short thorns in their mid-length, and though the thorns are not very thick, they surely are much thicker and stronger than all other setae and spurs that can be found on this chironomid body. Profemora 210 μm long, meso- and metafemora ca. 260 μm long. Femora bare, but meso- + metafemora do have a structure resembling apical spur. The spur shape is uncertain, the "spurs" seem short and could be only caused by leg bends. Protibiae unarmed. Meso- and metatibiae bear small spur, or if there are two spurs, they are so close to be called as single spur. All tibiae and tarsi are gently covered with setae, hardly visible in microscope. Protarsi five-segmented, ended with two claws and tiny empodium. Wings poorly preserved.
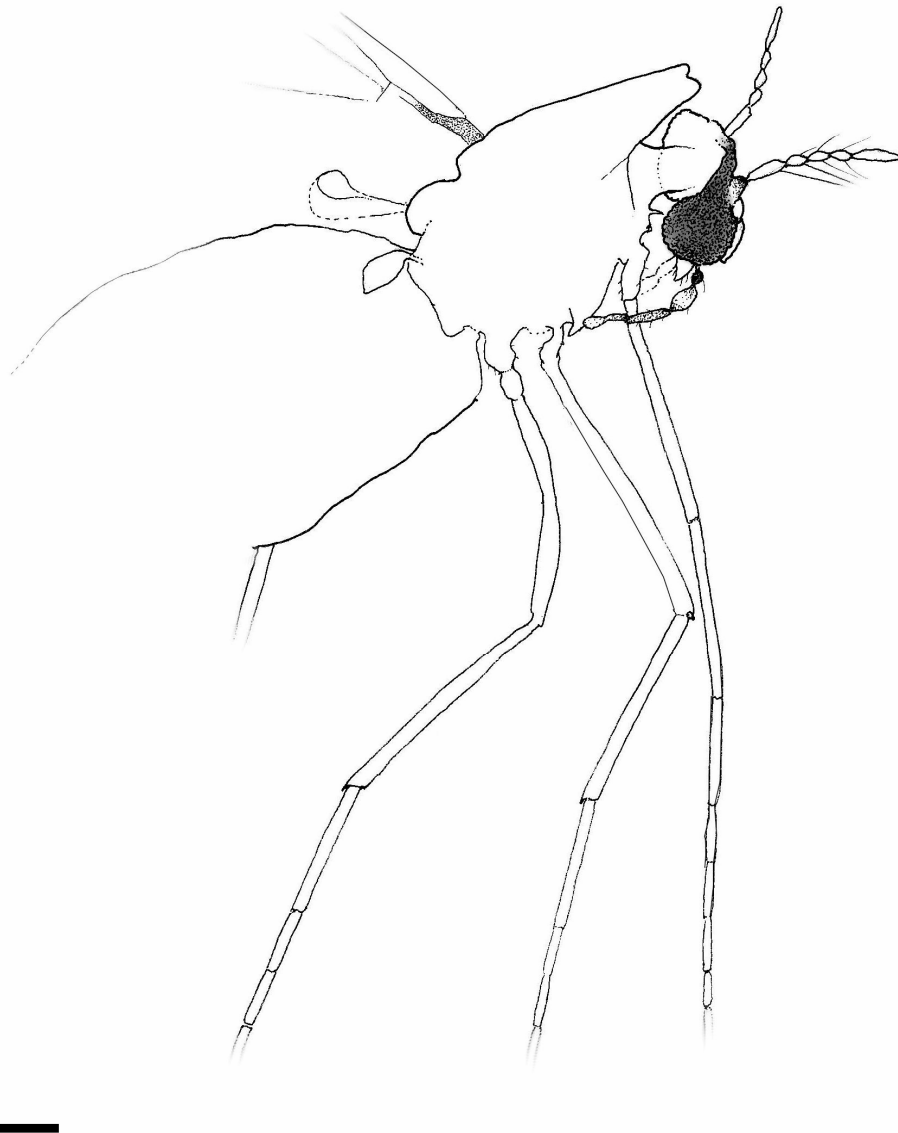
Fig. 25. – Chironomidae (genus et species indet.) from no. 11, scale bar: 100 μm.

Discussion. Determination of this fossil fly has been tricky. It can be considered as member of family Chironomidae, with tenative affinities to subfamily Orthocladiinae Lenz, 1921. But since many chironomids are better known as larvae, than much shorter-living adults, it is not easy to compare the features found on this specimen with extant members of Chironomidae. This fossil fly is clearly a female. The large dark abdomen can be even full of eggs. Antennae consist of only 7 antennomeres and they bear only

subtle setae. Generally, the antennae are strongly sexually dimorphic within Chironomidae (see figures in Stur & Ekrem 2020), with males having long, pulmose antennae and females with much more inconspicious, shorter antennae (Armitage et al. 2012). This fossil fly has 5 flagellomeres, of which first and last are longer than the three in between. Similar situation exists e.g., in genus *Thiennemanniella* Kieffer, 1918 (Orthocladiinae) (Sæther 1981), *Smittia* Holmgren, 1869 or *Ortocladius* van der Wulp, 1874 (also Orthocladiinae) (Stur & Ekrem 2020) and probably many others. Further characters common for females of Orthocladiinae are: prominent ommatidial lenses, short mouthparts, slender legs with very short coxae, five palpomeres (see Sæther 1981). Antennae of this form can not be found out of Chironomidae, so at least the family can be stated with certainity with note that there are some significant key characters shared with Orthocladiinae.

Many chironomids are much better known as (often extremotolerant) larvae and their description and determination is mostly focused on larval stages and larval morphology. Larvae are almost in all cases aquatic, inhabiting various water bodies. The only chironomid subfamily containing species with wholly terrestrial life cycle is Orthocladiinae (Armitage et al. 2012), but in case that Orthocladiinae have aquatic larvae, they are often found in running waters (Pillot 2013). Terrestrial larvae can feed on wood, algae and mosses, or they can be scavengers (Pillot 2013).

There is evidence of fossil chironomids found in the Lower Cretaceous of Lebanese amber attributed to the subfamilies: Orthocladiinae, Prodiamesinae Saether, 1976 and Tanypodinae (Veltz et al. 2007). Other Lower Cretaceous taxa were described from the Wealden amber, Isle of Wight, which are attributed to Laurasian subfamily Buchonomyiinae Brundin & Sæther, 1978 , i.e., genus *Dungeyella* Jarzembowski et al. 2009 (Jarzembowski et al. 2008). Burmese amber provides a male specimen of Orthocladiinae; *Myanmaro* Giłka et al., 2019 (Giłka et al. 2019), but further members of this non-biting midge subfamily are not known from Myanmar. Much more species were discovered in the Eocene amber. In French Oise amber, 60.3 % of 841 specimens of chironomids were identified as members of Orthocladiinae (Doitteau & Nel 2007). Orthoclads occur also in the early Eocene of Fushun amber (China) (Wang et al. 2014), in Sakhalin amber (Baranov et al. 2015) or Baltic amber (Baranov et al. 2015). Last but not least, there is evidence of a chironomid pupa (also placed in Orthocladiinae)

described from the Rovno amber in Ukraine (Andersen et al. 2015).

Infraorder: Culicomorpha

Superfamily: Chironomoidea

Family: Ceratopogonidae

Subfamily: Forcipomyiinae Lenz, 1934

Atrichopogon **sp.** Kieffer, 1906 **(fig. 28 – B)**

Material. No. 218 - syninclusion of imagines of biting midge and fungus gnat in clear, half-cylindric amber piece. Both specimens are captured close to the perimeter, close to each other but not in contact.

Description. Body 0.9 mm long, hairy, well sclerotised. Head 160 μm long and 200 μm high. Palps 5- segmented, but first two segments not discernible, the third segment enlarged. Antennae with 15 antennomeres. Scape not discernible, pedicel large and globular, wider than all flagellomeres. First 9 flagellomeres (F1-F9) very similar in size, ca. 15 μm long, oval and of similar width. F9 - F12 elongated. F9 and F10 ca. 40 μm long, F11 50 μm long, F12 65 μm long and ended with small nipple. Antennae, vertex, occiput, frons, palps and terminal mouthparts covered with setae. Long setae present on antennal flagellomere (F11) about 75 μm long. Last four flagellomeres bear several long setae on their base and numerous shorter setae, in contrast to F1-F8, where most of setae are equal in length (up to 70 μm). Thorax 310 μm long, convex, scutum well-sclerotised. Dorsum setose. Wings 760 μm long with large amount of microtrichia and only minimum macrotrichia. Row of hairs on posterior wing margin is simple, composed of shorter and longer (ca. 40 μm) setae alternating. The hairs in this row are straight. C ending in about 2/3 of wing length, when meeting the ending of R4+5. R1 conjunction with C almost viewless. R 2+3 forking from R4+5 and joining R1. M1 and M4 vanishing. Further venation could be estimated only by lines lacking macrotrichia. Legs unarmed except of ubiquitous hairs. Tarsi 5-segmented, empodium present, triangular. Tarsal claws curved. Procoxae 150 μm long, profemora and protibiae 210 μm long, protarsi 300 μm long. Mesomemora 260 μm long, mesotibiae as well. Metafemora 300 μm long, metatibiae 320 μm long, metatarsi 330 μm long. First tarsomere on hindlegs more than 2x long as the following tarsomere. Abdomen 420 μm long, hairy, bearing female genitalia.

Discussion. This small-sized biting midge is a representative of genus *Atrichopogon* Kieffer, 1906 after the following combination of characters compared to Wirth et al. (1974): Female antenna 15-segmented; empodium well developed; tarsal claws curved. Microtrichia on wing large and conspicious; macrotrichia when present not scale-like; fringe on posterior border of wing simple; a single row of alternating hairs; costa reaching well beyond midwing. Because of the possible confusion with *Forcipomyia* Meigen, 1818 (both genera for example have a small nipple on the terminal flagellomere), it is necessary to focus on other features. The characters compared with characteristics of *Atrichopogon* after Ewen & Saunders (1958): hing basitarsus always at least twice as long as the second tarsal segment, macrotrichia less dense than in *Forcipomyia*, costa reaching to 2/3 of wing length. The most important distinguishing sign is the character of marginal wing fringes, which is on the posterior wing margin and composed of straight hairs of two different sizes. The fossil *Atrichopogon* from Študlov is unusually hairy, resembling *Forcipomyia* in general, but differing in many structural details.

Adult representatives of genus *Atrichopogon* have various food strategies, such as sucking body fluids of beetles (Meloidae and Oedemeridae). Some of their relatives from Forcipomyiinae suck the haemolymph from dragonfly or butterfly wing veins, attack carterpillars etc. This predatory strategy occurs within females and the prey is often similar in size as the predator or much larger. But both sexes use to visit sources of sugar, species of *Atrichopogon* often visit flowers and function as pollinators, sometimes also feeding on fluid content of pollen grains (Downes 1955).

To this date, the oldest-known *Atrichopogon* comes from the Eocene of Baltic amber. *Forcipomyia* has a similarly long fossil record, appearing in early Eocene of Indian Cambay amber (Stebner et al. 2017) and the mid Eocene of Sakhalin amber (Szadziewski 2008, see also Baranov et al. 2015). According to Szadziewski et al. (2016) the biting midges (Atriculicoidini Szadziewski, 1996) found in the Lower Cretaceous of Spanish amber could represent older relatives to later Forcipomyiinae Lenz, 1934. Life strategies of adults in genus *Atrichopogon* still stay a bit enigmatic. This fossil biting midge, suspiciously embedded together with a fungus gnat, could have been trying to

feed on an easy prey which was trapped in fresh resin. But it could have searched for another liquid food or visit its future trap randomly.

Infraorder: Bibionomorpha

Family: Anisopodidae Knab, 1912

Mycetobia **sp.** Meigen, 1818 **(figs. 26; 27).**

Material. No. 124 - Transparent amber piece with lenticular pseudoincluisons that aggravate the possibilities of the inclusion observation. There is a main inclusion - an adult specimen of wood gnat, and two other syninclusions - certainly insects, but rather incomplete. The wood gnat is almost complete, except of its right wing that had to be polished in order to get access to the other wing. The left wing is greatly preserved, but wing base obscure due to level of preservation.

Description. Body 2.7 mm long. Head, though formerly well sclerotised, now compressed to a discoidal surface. Antennae 1 mm long, bent bluntly upwards in their half, consisting of 14 antennomeres. None of the flagellomeres with special structures, nor enlarged, except of the terminal flagellomere, which is almost three times longer than the previous one, but not thicker. Head 600 μm high. Thorax round, almost globular, 800 μm long. Abdomen cylindrical, but pointed at the end, 1.7 mm long, dorsal side bearing mid-dense setose covering. Wing 3.4 mm long. Venation not reduced. Wing margin with short setae. Veins C, Sc, R1, R2+3 and R4+5 thickened. There is a short thickened section of the wing margin, following the connection of C and R4+5. M forked into two branches. CuA2 thickened, discoidal field present, large. There is a faint trace of claval furrow between CuA2 and A1, which could, however, easily be an artifact. Coxae large, ca. 600 μm long. There is a gap between procoxa and coxae II+III. Metafemur 800 μm long. Metatibiae approximately as long as femora.

Fig. 26. – *Mycetobia* sp. (Anisopodidae) from no. 124, scale bar: 1 mm.
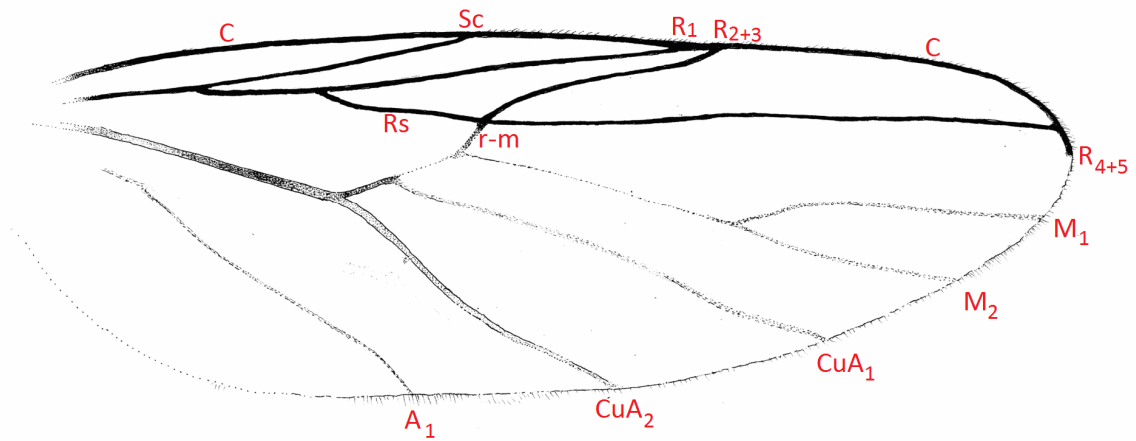

Fig. 27. – Wing of the *Mycetobia* sp. (Anisopodidae) from no. 124.

Discussion. The only inclusion from this amber piece that can be determined at least to family level is this wood gnat of genus *Mycetobia*. The family Anisopodidae is

characteristic by disctinct flagellar segments, the Rs vein forking at or just before the r-m crossvein and no great modifications of antennomeres (Oldroyd 1954). Members of this family should be at least 3 mm long. This fossil *Mycetobia* is slightly shorter, but it can be assumed that it would reach the length of 3 mm, if its head was not collapsed. Thorax of Anisopodidae is convex with scutum and scutellum setose, bristles only weakly developed. Position of the Rs fork is a good key to distinguish between families Anisopodidae and Mycetophilidae, because mycetophilids have R4 fork distal to r-m crossvein (Hancock and de Souza Amorim 2009). All these characters can be observed in our fossil. The wing venation of specimen from Študlov fits to *Mycetobia* (also *Neomesochria* Amorim & Tozoni, 1994) - wing without discal cell, M clearly 2-branched (Hancock and de Souza Amorim 2009). Vein Sc is distinctly present, terminating in C; M1+2 present; A1 distinct, terminating in posterior wing margin (Thompson 2006). Vein R2+3 is not reaching R1; the opposite situation could be found in genus *Mesochria* Enderlein, 1910 (Thompson 2006).

Larvae and adults of extant *Mycetobia* species are associated with tree sap exudations (Hancock and de Souza Amorim 2009). This fact could increase the chance of capturing some specimens in fresh resin.

There is no older representative of *Mycetobia* than a species described from the mid Cretaceous Burmese amber (Myanmar) as *Mycetobia myanmara* Kania et al., 2019 (Kania et al. 2019). However, this genus became far more abundant during the Eocene. Wojtoń et al. (2019) provided a review of numerous representatives of *Mycetobia* in the Eocene ambers with descriptions of new species. Above all species, *Mycetobia connexa* Loew has been found most frequently. Another species as *Mycetobia perkovskyi* Wojtoń, Kania & Krzemiński, 2019, comes from Ukrainian Rovno amber, while the others are from the Baltic amber. Most of them were determined as females. Grimaldi (1991) found genus *Mycetobia* in the Dominican amber together with pupal exuviae typical for this genus.

It is an interesting contrast: while the previous genus *Leptoconops* has been mostly known from the Cretaceous ambers, the genus *Mycetobia* is better known from Paleogene deposits.

Infraorder: Bibionomorpha

Superfamily: Sciaroidea

Family: Keroplatidae Rondani, 1856

Subfamily: Keroplatinae Rondani, 1856

Tribe: Orfeliini Matile, 1990

Genus et species indet. (figs. 21 – C; D)

Material. No. 218 – syninclusion of imagines of biting midge and fungus gnat in clear, half-cylindric amber piece. Both specimens are captured close to each other but not in contact.

Description. Body 1.53 mm long. Head round, 160 μm long, 215 μm high. At least one lateral ocellus present. Compound eye almost round with shallow invagination laterally from antenna. Vertex and postgena with short dark setae. Frons and face non-setose. Antenna with 17 antennomeres. Flagellum apically slightly tapering, with 15 flagellomeres. Flagellomere 1 1.5x wider than long, following flagellomeres longer than wide. Flagellum with pubescence about half of segment's width. Palps 5-segmented. First two segments discernible. Third segment cylindrical, with sparse dark setae, fourth segment apically widening, bearing sparse dark setae. Fifth segment tapering, about 3.5x as long as wide basally. Scutum convex, with distinct dorsocentral, acrostichal and lateral setae. Scutellum with eight short setae along its margin. Proepisternum bearing one seta, anepimeron and anepisternum setose, metanotum bare as well as pleurotergites. No posterior spiracular hair. Wing 1.54 mm long and 600 μm maximum width. Wing membrane covered with light brown microtrichia. C and R veins thicker and slightly darker. R1 and R5 with macrotrichia dorsally. Sc ending in C well distal to level of Rs. Rs oblique, slightly longer than r-m. Tb well visible. R5 nearly straight. M4 and Cu1 setose, Cu1 reaching wing margin; Cu2 fold like, in basal 2/3 distinct, in apical 1/3 pale, apically approaching Cu1 and not reaching wing margin. A1 short, indistinct, apressed to Cu2. Haltere pale. Tibiae and tarsi with dense setae, procoxae 360 μm long with anterior setae on its entire length. Mesocoxae 380 μm long, with anterior setae on apical half.

Metacoxae 350 μm long, less pilose, almost bare. Femora entirely covered with short dark setae. Mesofemora 580 μm long. Tibiae apically slightly widening with setae not in rows. Protibiae bearing an apical comb of setae near spur. Mesotibiae 590 μm long without the comb, but with 3-4 apical setae. Tarsal claws small. Abdomen small, dorsoventrally flattened, about 1mm long, genitalia not apparent.

Discussion. After the key to subfamilies and tribes of Matile (1990: 125, 190), this fossil fungus gnat is not member of neither Arachnocampinae Matile, 1981, neither genera *Asynaphleba* Matile, 1974 and *Paleoplatyura* Meunier, 1899, because of radio-median fusion. It also does not fall into Macrocerinae Rondani, 1856 because of the absence of a cerebral sclerite and flagellomeres are not so elongated.

On the contrary, the presence of apical combs on fore and mid tibiae place this fossil into the tribe Orfeliini, as well as its well developed mouthparts (palpifer + four palpomeres). There is an ambiguity with the wing venation, as the absent R4 and reduced A1 are more typical for Keroplatini, see *Asiokeroplatus* Ševčík, Mantič & Blagoderov, 2015, *Chetoneura* Colless, 1962, *Microkeroplatus* Ševčík & Papp, 2009 and *Pseudochetoneura* Ševčík, 2012. However, the division of Keroplatinae into Keroplatini and Orfeliini has been doubted by some authors (Ševčík 2012, Kurina et al. 2017). This fossil fungus gnat also differs from other Orfeliini with its mouthparts, which are not reduced, thus will be described as a new genus and species, due to further characters making its unique position among Orfeliini.

No Orfeliini have been found in the Cretaceous fossil record. However, they were diverse and quite abundant in the Eocene epoch. Members of this tribe were found in early Eocene Indian amber (Solórzano Kraemer & Evenhuis 2008), in Baltic amber (e.g. Meunier 1904), but also in the Miocene of Dominican amber (Penney et al. 2013).

Suborder: Brachycera

Superfamily: Platypezoidea

Family: Phoridae Curtis, 1883

Genus et species indet. (fig. 28 – E).

Material. No. 35 – formerly large dark amber piece, dark and obscure, almost non-transparent. A small transparent fragment containing an adult phorid fly was separated and polished. The two larger fragments do not contain anything except of an isolated

insect leg, which is poorly preserved.

Description. Body 1.4 mm long, strongly sclerotised, well preserved. Head hypognathous, ca. 280 μm long and 400 μm wide, bearing bristles (or thick capitular setae). Frontal bristles are shorter than vertical, which are the longest, and both of them are longer than occipital comb of setae which adjoins posteriorly to compond eyes. Antennae with first flagellomere elongated, hiding scape and pedicel. Arista filamentous, 500 μm long. Mouthparts small, proboscis short. Thick short setae also on ventral side of the narrow part of prothorax. Antennae with only basal parts discernible. C thickened until connection with vein R4+5, the thickened part bearing prominent erected setae. Sc weak and joining the thickened R1, together both ending in C. The last thickened vein Rs forks into R2+3 and R4+5 shortly before reaching C, Rs bare. Rest of the wing is unclearly preserved with only discernible proximal parts of veins M1 and M2. Thorax ca. 700 μm long, notum hairy. Abdomen very short. Legs armored. Profemora ca. 800 μm long, without enlarged setae. Protibiae 400 μm long, one spur in 1/4 of the tibial length, two spurs apically. Protarsi 5-segmented, segments shortened gradually. Mesomefora ca. 700 μm long, mesotibiae 400 μm long, two spurs in 1/4 of tibial length, one large spur apically. Mesotarsi 850 μm long, 5-segmented. Metafemora 600 μm long, nut thick ca. 250 μm wide. Metatibiae 800 μm long, one spur in 1/4 of tibial length, two long spurs apically and a few shorter. Metatarsi 1mm long, tarsomeres shortening gradually. Empodium on all tarsi thin or not discernible.

Discussion. As stated by Disney (2012) and Oldroyd (1954), Phoridae or scuttle flies are typical with their reduced wing venation. Disney (2012) calls C and R "thick veins". They are shortened, ending far before the wing apex. "Thin veins" join them, but the base of M1 and M2 often seems to be weak and unattached. Metatarsi bear transverse combs of hairs. This fossil fly is clearly a member of Phoridae. Further identification is unfortunately complicated. The bare Rs, branching distally into R2+3 and R4+5, represent a certain diagnostical value, as well as tibial and tarsal setae, however the hardly-visible antennal structure, frons and mouthparts make further identification difficult.

Phoridae represent a fly family with diverse food strategies. Most often they seek for dead arthropod bodies or various liquid food, often containing sugars (Disney 2012).

Despite not much can be said about this scuttle fly, it has three relatives described previously from Študlov amber (Prokop and Nel 2005). *Pararhoptrocera moravica* Prokop & Nel, 2005 is larger in size (2 mm) and has more prominent mouthparts, in contrast to much shorter legs, but the number of spurs (bristles) on basal 1/3 of tibiae fits well. *Anevrina huberti* Prokop & Nel, 2005 has hairs on Rs, and the numbers of tibial bristles, which differ from our fossil. *Aenigmatistes studlovensis* Prokop & Nel, 2005 is similar in size (1.25 mm), Rs bare, bearing a short proboscis, but arista seem to be thicker than in this fossil specimen. Numbers and positions of tibial spurs are unknown.

Besides these three fossils from Študlov, there are many other phorids found in amber, since the mid Cretaceous. Represetatives of *Priophora* Robineau-Desvoidy, 1863 were found in Canadian amber (Brown & Pike 1990), *Euliphora* Arillo & Mostovski, 1999 of the same subfamily (Prioriphorinae Mostovski, 1996) is described from Spanish amber (Arillo & Mostovski 1999). Also in French Cretaceous amber, the genus *Priophora* is present (Solórzano Kraemer et al. 2011). In Eocene, the diversity of fossil scuttle flies markedly increased. There are genera as *Anevrina* Lioy, 1864, *Dohrniphora* Dahl, 1898 or *Triphleba* Rondani, 1856 all known from the Baltic amber (Brues 1923, Poinar 2003, Brown 2013), and the latter (*Triphleba*) also found in the Rovno amber (Perkovsky et al. 2015).

> **Fig. 28.** – Flies of Študlov amber. **A,** Chironomidae (genus et species indet.) from no. 11, scale bar: 200 μm. **B,** *Atrichopogon* sp. (Ceratopogonidae) from no. 218, scale bar: 500 μm. **C, D** Orfeliini (genus et species indet.) (Keroplatidae) from no. 218, scale bar: 1 mm. **D,** habitus, scale bar: 500 μm. **E,** Phoridae (genus et species indet.) from no. 35, scale bar: 1 mm.
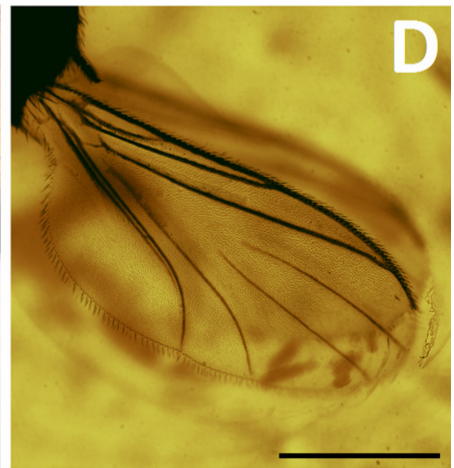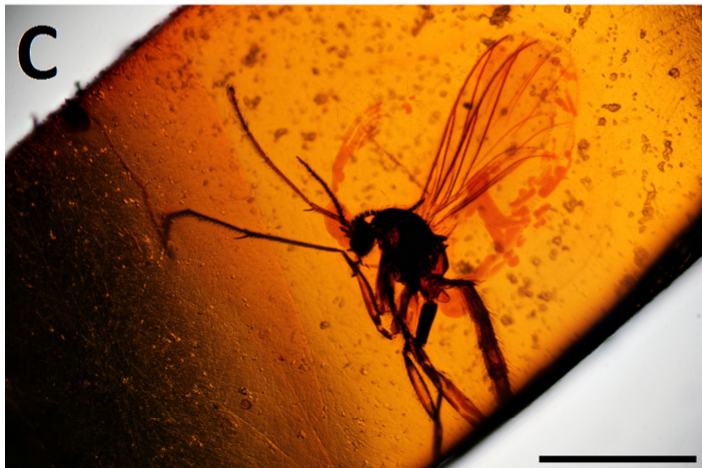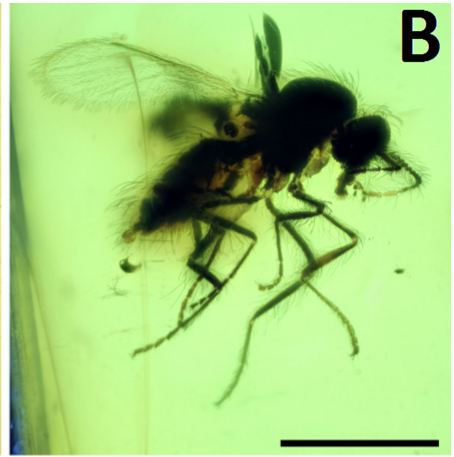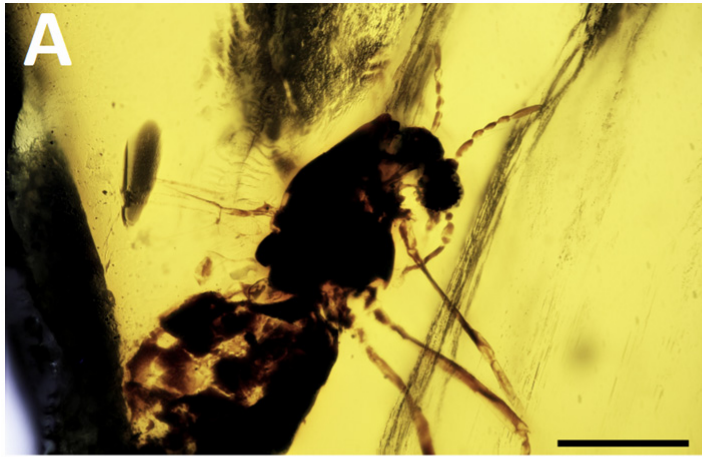
5. Discussion

5. 1. – General composition

The Študlov amber deposit, so far the only source of amber with biological inclusions in the Czech Republic, reveals high diversity of fossil organisms. Only a few of them had been investigated during the past years, including 6 species of flies (Nel & Prokop 2004, Prokop and Nel 2005, Tkoč et al. 2016) and one scelionid wasp (Nel & prokop 2005). The amber resin had been collected by Jakub Prokop and his students and colleagues from Charles University for more than two decades. The raw material was stored and waiting for the treatment and detailed evaluation. In 2017, the collected material was sorted by the author and processed by cleaning, polishing, documentation and determination of each biological inclusion.

Študlov amber shows variety of biological inclusions: over 50 plant specimens including one pleurocarpous moss, seven different trichomes, one fragment of gymnosperm twig and 29 specimens of wood tissue. Fungi are represented by 33 specimens as mostly spores (ascospores), simple mycelia, dark thickened mycelia and several „ichnofossils", which occurred when the original fungal mycelium decayed and only tunnels remained preserved in amber. A single nematode was found in syninclusion with an incomplete insect body and bifurcate plant trichome. Vertebrate fossils are generally extremely rare and none was found in our amber. Most numerous were arthropod inclusions: 62 specimens. 4 non-parasiting oribatid mites (Oribatida: Brachypylina), various incomplete body parts (wings, legs), one beetle (Latridiidae), one sample containing butterfly scales, one specimen of scale insect (Coccoidea: Eriococcidae), one bug (Heteroptera: Miridae). one cicad exuvia (Cicadomorpha), two barklice (Archipsocidae), two thrips (Thripidae), ten hymenopterans (Scelionidae, Chalcididae, Pteromalidae, Formicidae, Stigmaphronidae) and 24 flies (Ceratopogonidae, Chironomidae, Keroplatidae, Phoridae, Anisopodidae and *incertae sedis*). Furthermore, there are still some inclusions of clearly organic (biological) nature, which can not be identified.

5. 2. – Characteristics of the amber

These numbers of collected specimens are certainly not definitive. The sandstone-claystone layers along the Brumovka stream still can expose coal beds with new amber layers. Some new outcrops can be found during building activities or logging, while the old outcrops slowly disappear.

Today, mostly small amber pieces are being found. The biggest pieces in the collection are only about 3 cm long. Some of these pieces are easy to break, even accidentally, as they often fall apart along the amber layers. Carefulness is necessary when handling with the material. The raw amber is dark and opaque and can be mixed with the soil, but most of the fragments become transparent after water cleaning and polishing. Some of these fragments stay dark, which is caused by high inner concentration of organic material. In this case the resin was probably mixed with the forest ground before hardening.

The each inclusion significantly differ in the quality of preservation. Sometimes there is only a trace of the fossil organism. Some fossils, on the other hand, have been preserved in perfect condition. There is a feature shared by nearly all Študlov fossils: very small size. The insects trapped in the Študlov amber are rarely longer than 1.5 mm. And if so, in case of arthropods, then the body is usually incomplete. The amber seems to be produced by the source plant only in small amounts, which concerns the resin on the tree surface that could interact with other organisms. Larger amber pieces are supposed to originate in the inner tissues. There is a simple correlation: the smaller amber droplets are produced, the smaller are the inclusions that will become embedded, not managing to fall off or escape.

5. 3. – The plant producer

As the plant producer of Študlov amber, angiosperms were considered primarily by Mátl et al. (1999), judged by the presence of oleanane, determined by the gass chromatography/mass spectrometry. As the authors stated, oleanan is a biomarker occurring in rocks younger than the Upper Cretaceous and its source was attributed to the angiosperms. This conclusion was later doubted by Havelcová et al. (2014), who

investigated various Czech fossil resins from Cretaceous, Paleogene and Neogene also by gass chromatography/mass spectrometry. Due to the presence of labdan type diterpenoids and the absence of plant triterpenoids, incl. oleanane, all of the Czech fossil ambers were produced by conifers of Cupressaceae, incl. duxite, which might be produced by *Glyptostrobus* or *Quasisequoia*. However, Mátl et al. (1999) do not suggest the angiosperms as the source plant due to absence of succinic acid in the resin, as Havelcová et al. (2014) claimed, but because of the presence of oleanane. Later, Havelcová et al. (2019) did not find enough specific biomarkers for the conifers in two samples of the amber, hence considering rather a mixture of conifer biomarkers with nonspecific (angiosperm or gymnosperm) terpeonids. Since both assumptions seem valuable, it would be much benefitial to execute further analysis, based on multiple samples of Študlov amber.

The remains of woody tissues of gymnosperms found in Študlov amber definitely outbalance the number of samples containing angiosperm or probable angiosperm wood. It is hard to tell if the angiosperm vessels demonstrated in the specimen no. 114 were part of a tree xylem. The most promising fossil wood is the specimen no. 233. This single fragment of gymnosperm twig probably came from the amber tree. The way of its preservation supports this hypothesis: the concentration of resin pervasion increases in outer layers of the twig. If the twig fell from a random plant and then was trapped in fresh resin of another plant, then the resin would pervade the cells equally all around and on the transverse section, which is not this case. The central pith cells keep nearly free from the resin. What is more surprising, the twig preserved in its original form - not as an amber inclusion, not embedded in resin. Presumably it is determined as *Glyptostrobus* or a related plant species from Cupressaceae, from which the twig comes from*,* but *Doliostrobus* (Doliostrobaceae) can not be excluded as well, being also a part of European Eocene forests (Kvaček 2010). When observing the wood structures under optical microscope, this fossil twig shows marked similarities of cross field pits as the samples of *Glyptostrobus lineatus*, kindly provided by Jakub Sakala for the comparison.

Glyptostrobus is an interesting conifer genus, currently restricted to small populations in South-eastern Asia (LePage 2007). The survivor trees are typical for various waterlogged ecosystems, with altitudes reaching up to almost 2000 m, not tolerating alkaline and saline soils or water and being sensitive to aridity rather than low

temperatures. The fossil distrbution of *Glyptostrobus* is impressive: it began to spread in the early Cretaceous from what is today called North America, finding its way to Eurasia in Cenomanian, but disappearing from fossil record from European Late Cretaceous. It returned to Eurasia during the Paleocene and became widespread during Eocene in Europe. The genus shows a distribution pattern coincident with orogenetic processes, implying certain level of disturbances. The Oligocene cooling and climate change caused the retreat of *Glyptostrobu*s (LePage 2007). The same author also suggests that the remaining ecosystems with occurrence of *Glyptostrobus* could be similar to those known from the fossil record. It is easy to imagine that this kind of tree could produce resin that later preserved in mud without oxygen, and after millions of years became fossilized as amber. However, as said in chapter 4. 1. 2., even if *Glyptostrobus* was not the real producer of resin, its occurrence offers an interesting paleoecological context.

5. 4. – Age of Študlov amber

The Western Carpathians arose thanks to the processes of Alpine orogeny, which has been hugely affecting the European continent since the Late Mesozoic. The Beloveža Formation of Bystrica unit, in which the amber is being found, is somewhere between upper Paleocene (57 Myr) to mid Eocene (Lutetian, 47 Myr) old, but occasionally referred also as late Eocene (Golonka & Waśkowska 2012). The Študlov amber is traditionally dated to the lower or mid Eocene (Mátl et al. 1999). The development of Outer Western Carpathians was running mostly during Paleogene (Plašienka et al. 1997), the "core mountains" gained their shape in early Miocene. The Bystrica unit is a part of Magura belt, which is the almost outermost belt of Outer Western Carpathians, just after the Krosno belt. During Paleogene, it was affected by downwarping of the flysch sedimentation (Plašienka et al. 1997). The Magura belt is formed by rocks of the former Magura basin, which began to arise in the upper Eocene. In Magura belt, signs of Cretaceous deep-oceanic sediments occur (Oszczypko 2006). However, while the Carpathian orogeny is a complicated process, the Bystrica unit seems to be part of tentonically calmer Magura belt (see Plašienka et al. 1997).

Mátl et al. (1999) confirmed the age of Študlov amber as "younger than Upper Cretaceous", based on presence of oleanane detected by the gass chromatography/mass

spectrometry. Havelcová et al. (2016) also considered the amber as of Eocene age. Having an overview of biological inclusions from this amber, the comparison offers some indicia. There are basically two fossil insects which questioned the Eocene age. The most conspicuous is the stigmaphronid wasp (no. 263). Stigmaphronidae (Apocrita) were considered as an exclusively Cretaceous family (Engel & Grimaldi 2009). However, this single stigmaphronid is diffilult to compare to the known genera of this family. The Eocene ecosystem of Študlov amber forest could represent a refugium for the surviving stigmaphronids. The second case is the *Leptoconops* (Ceratopogonidae), showing high fossil diversity during the Cretaceous, compared to only a few Eocene records (Szadziewski et al. 2015, Stebner et al. 2017). But *Leptoconops* is an extant genus with tens of known species, so its sparse occurrence in the Eocene does not seem to be problematic. Finally, Tkoč et al. (2016) described a dolichopodid fly *Microphorites moravicus* from Študlov amber, which also questioned the Eocene age. However, only a year later, Bramuzzo & Nel (2017) described *Microphorites erikai* from the Eocene Oise amber. Hence these are the first two records of genus *Microphorites* in Eocene.

In contrast, neither the presence of family Archipsocidae (Psocoptera), nor Myrmicinae (Hymenoptera) has been proved in the Cretaceous fossil record so far.

In the middle Eocene Climatic Optimum (MECO), the European deciduous vegetation found ideal conditions for growth. In early to mid Eocene, the vegetation was probably divided into three main types: the polar deciduous forest, paratropical seasonal forest and the evergreen, broad-leaved forest. While the evergreen, notophylous forest covered eastern part of the West European platform incl. Bohemian Masiff, the paratropical forest grew on its western half. The polar, deciduous, but still angiosperm-dominated forest was typical for the Fennoscandia (Kvaček 2010). It would be easy to suggest that the Študlov amber forest could be gymnosperm-dominated and thus its age is the cooler upper Eocene when conifers began to dominate again, but it is not necessarily true. The amber forests usually form kind of azonal vegetation, for which the rules vary. In addition, the Študlov forest grew on the outline of the forming Carpathians, which means it was not part of the "continental" forest of European platform, divided from it by shallow sea.

Coming back to the chronostratigraphic aspects, there is no problem spanning the age of Študlov amber from early to mid Eocene (Ypresian to early Lutetian 47 Myr). That would make a nice parallel to the lowermost Eocene French Oise amber, and also other two slightly younger ambers of Baltic and Rovno from the Upper Eocene.

5. 5. – European Eocene ambers

The Eocene climate was unambiguously benefitial for amber production. In Europe there are several fossiliferous amber deposits: French Oise, Baltic, Ukrainian Rovno plus the problematic Bitterfeld in Germany. Instead of comparsion of Študlov amber with the Baltic deposit, which provides vast diversity of all kind of organisms, it seems more useful to name the fossil taxa shared by other known deposits.

The oldest of them is the amber from Oise, France. Its age is Ypresian, Lower Eocene, about 53 Ma (Penney 2010). The comparsion of the French amber and the Czech amber began in 2004, when Nel & Prokop described two new scatopsid flies: *Paraectaetia ruckii* from Študlov and *Cookella eocenica* from Oise. A year after, Nel & Prokop (2005) described two new scelionid wasps, *Galloscelio* from the French amber and *Moravoscelio* from the Czech amber. Psocopterans in Oise amber are represented by various Troctomorpha and Trogiomorpha, in contrast to the only archipsocid, which was determined as *Archipsocus puber* Hagen, 1882 (Nel et al. 2005). The only determined barklouse from the Študlov amber is an archipsocid, most probably *Archipsocus* as well. The Cecidomyiidae genus *Lestremia* Macquart, 1826 is also shared within both ambers. Plant producer of the French amber was probably an angiosperm genus *Aulacoxylon* (Fabaceae) (Kirejtshuk & Nel 2013) or *Hymenaea* (Fabaceae) (De Franceschi & De Ploëg 2003). But in time when the Paris basin was already a part of European plate, the Western Carpathians were still at the beginning of their formation, divided by not-so-shallow seas from Western Europe. This geographical bareer was only surmountable by species with high dispersion potencial (flying species, ligh-seed plants etc.).

The Ukrainian Rovno amber is a rich deposit with age estimated about 35 Ma (Penney 2010). Szwedo & Sontag (2013) insisted on the same origin of Baltic, Rovno and Bitterfeld ambers and their later transportation thanks to Pleistocene glaciers, judged after the species composition of biting midges (Ceratopogonidae). However, though

there are common features of these ambers, perhaps the origin of these ambers shall not be judged by presence of flying insects, which are easy to disperse. Other authors keep finding divergences, despite they admit parallel origin of these ambers in different localities (Perkovsky et al. 2007, Mänd et al. 2018). Returning to Študlov amber in comparsion with Rovno amber, they share the beetle family Latridiidae (Sergi & Perkovsky 2014), wasp families Pteromalidae and Scelionidae, and also dipteran families Keroplatidae, Cecidomyiidae (subfamily Lestremiinae), Phoridae, Anisopodidae, Ceratopogonidae and probably more (Perkovsky et al. 2003).

The Bitterfeld amber, even if considered as redeposited Baltic amber, is reffered as younger - 23 Ma, uppermost Oligocene (Standke 2008). It will be mentioned here only briefly, because it is known mostly with its liverworts (Heinrichs et al. 2016) and diverse fungi (Schmidt et al. 2013).

The mid Eocene Sakhalin amber lies in the far east of Russia, but it would be a shame not to mention this deposit at least (Fedotova & Perkovsky 2016). It and has not been so rich in biological inclusions as e.g. Rovno amber, however there are some connections with Študlov, as the chironomid family Orthocladiinae (Baranov et al. 2015), chalcid wasps (Simutnik 2014) and ceratopogonid family Forcipomyiinae (Szadziewski & Sontag 2013).

Finally, it is not the point of this chapter to forcingly look for the most similar amber deposit. Presumably the locality Študlov was isolated and not connected to any of the named localities (see visualisations on Deep Time Maps™ 2020). The ancient locality itself was part of the nascent Western Carpathians, separated from the mainland by the sea.

5. 6. – Reconstruction of paleoecosystem

Despite the quality and quantinty of Študlov amber, the available fossils are not sufficient to provide us a detailed image of this Eocene ecosystem. At least the following observations were considered. The gymnosperm twig shows annual rings on the transverse section, proving that there had to be certain seasonality in the forest: either cooler annual periods, either related to precipitation. And once again, if we identify the

twig as *Glyptostrobus*, there are some more indicia. According to LePage (2007), the glyptostrobes grew in various wet ecosystems following orogenetic processes, tolerating certain level of disturbance connected with the orogeny. We can imagine that the Študlov forest was not a coastal ecosystem, rather it grew in slightly higher altitudes, and this image is supported by Havelcová et al. (2019), who did not find any sodium enrichment in the amber, which would mean the contact with the saline marine water.

However, such conclusions have to be made carefully. The reader can probably imagine the Študlov forest as wet and humid, with mosses growing on the treebark, moss mites living in the canopy, ants crawling on the ground and *Leptoconops* larvae developing in wet soil. The amber producer plant might not be producing huge amount of the resin, but it had ideal conditions for being protected from its decomposition on the bottom of pools, related to the occurence of *Glyptostrobus*. Later it was exposed to tectonic processes, temperatures probably much higher than in case of Baltic amber (Mátl et al. 1999). The preserved stem rays in sample no. 33 can be produced by angiosperms or gymnosperms and are today more typical for tropical climate (Meier 2008).

Študlov amber might provide even more information for future researchers who armor with patience and keep searching for further material. Here, the first hypothesis on the amber-producing plant is suggested and the view of paleoecosystem is outlined.

6. Conclusions

Over 250 biological inclusions were found in the Eocene of Študlov amber from eastern Moravia, which is the only fossiliferous resin known from the Czech Republic. An overview of the significant fossil organisms is given, discussing their relationships to other taxa known from particularly Eocene amber deposits of Europe. The predominance of representatives of orders Diptera and Hymenoptera is confirmed and corresponds to other Eocene ambers. The specimen no. 263 contained a wasp of Stigmaphronidae, formerly known only from the Cretaceous period. Thus, the first Paleogene record of this family is demonstrated. The question of the age of the amber is discussed from various aspects. Except of the occurrence of the stigmaphronid wasp, no relevant reason seems to be for doubting the early to mid Eocene age for this amber. The presence of psocopteran family Archipsocidae and the ant subfamily Myrmicinae also confirms the Eocene age. An isolated stem fragment of a gymnosperm tree (Cupressaceae) was found and thanks to this discovery, the genus *Glyptostrobus* could be considered as the potential resiniferous tree. However, this should be proved by future studies. A few paleoecological ideas raised from this study: the paleoecosystem was a humid waterlogged forest with certain level of seasonality, not necessarily growing in coastal areas.

7. References

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