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In search for the unlikely: Leaf-mining caterpillars (Gracillariidae, Lepidoptera) from Upper Cretaceous and Eocene ambers

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Abstract

Fossil leaf-mining caterpillars from amber are firstly described as the new species *Phyllocnistis cretacea* from Upper Cretaceous Myanmar amber and *Phyllonorycter inopinata* from Eocene Baltic amber. Both show typical traits of leaf-miners, and specifically, of later instars of caterpillars of their respective genera. The findings give further evidence for these being quite old and conservative genera of Gracillariidae. These are basal Ditrysia which retained the larval feeding and mining live mode. The findings also represent direct fossil evidence of individual stages of hypermetamorphosis known from extant Gracillariidae. The finds from the Upper Cretaceous and their putative identifications give direct evidence for a minimal geological age for the genus *Phyllocnistis* (Phyllocnistinae) and, by indirect conclusion based on their divergence, also for the genus *Phyllonorycter* in a sister clade (Lithocolletinae). It also predates mining habit closer to the time of radiation of their angiospermous host plants.

Keywords

Introduction

Lepidoptera are exceedingly rare in the fossil record (Grimaldi and Engel 2005; Sohn et al. 2012, 2013). They are also rare in ambers which allow for a preservation of their delicate morphological structures which are needed for identification. As a working hypothesis for further studies in fossil Lepidoptera it was assumed that the larval stages of Lepidoptera, caterpillars, allow identification and geological dating of taxa not yet found as imaginal stages in ambers. This would be due to their different feeding and live mode, habitat, taphonomy but also their smaller size in comparison to the average size of ambers. Specimens not completely included in ambers are mostly destroyed by oxidation, breakage, abrasion, or other erosive processes. There is an obvious bias towards smaller inclusions (specimens), resulting for example for a strong overrepresentation of micro- versus macrolepidopteran inclusions. Focussing efforts with sample acquisition on larval stages of Lepidoptera from amber, a first member of

Geometridae from Baltic amber has been identified from such a caterpillar (Fischer et al. 2019). Leaf-mining caterpillars are quite small larval stages being internal feeders restricted in body size by their well-protected mode of living within leaves. Taphonomy of such internal feeders, this is inclusion of such larvae outside their habitat by liquid resin, seems a quite unlikely event. However, several taxa leaving their mines for pupation are known, e.g., *Anarsioses aberrans*, being set apart from *Phyllonorycter* as a new genus for this behaviour and differences in male genitalia (Davis 2019). Despite of long-term scientific studies in Baltic amber since the 19th century such inclusions of leaf-mining caterpillars had to date not been identified.

Leaf-mining Lepidoptera are of interest for several reasons. From the scientific point of view, they represent a primitive feeding and live mode found in many basal Lepidoptera families, which has been retained in a number of basal Ditrysia (a more derived group of Lepidopterans with respect to female genital organs) (Scoble 2002). Gracillariidae are a prominent family of ditrysian leaf-miners (Men-

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ken et al. 2009) and are exceedingly diverse (Nieukerken et al. 2011) with 101 genera and 1866 species. Economically, leaf-miners can become important pests of crop plants, especially for crops kept in monocultures.

Within the family Gracillariidae Stainton, 1854 the three subfamilies Gracillariinae, Lithocolletinae, and Phyllocnistinae had been recognized (e.g., Parenti 2000). A most recent molecular phylogenetic analysis, however, revises this to eight subfamilies (Kawahara et al. 2017). Imagos of putative Gracillariidae have been described from Baltic amber as *Gracillariites lithuanicus* and *G. mixtus* (Kozlov 1987). Palaeontological evidence for such caterpillars comes only from their leaf mines rarely preserved in some fossil leaves, mostly from the Neogene and Paleogene. However, oldest Lithocolletinae mines are from the Cretaceous (cf. *Cameraria* cf. *aceriella* Clemens, 1859 (Proc. Acad. Nat. Sci. Phil. 325) from the Dakota Formation (late Albian, Early Cretaceous) of Central Kansas; cf. *Phyllonorycter oliveirae* Martins-Neto, 1989 from the Ora Formation (Turonian, Late Cretaceous of Negev Desert [lithocolletiform mines]) (Krassilov and Shuklina 2008) (overview in Sohn et al. 2012, 2013). Mines of Phyllocnistinae had been dated to 99 +/- 10 m.y. (Wahlberg et al. 2013). The dating of the divergence of this sister subfamily to Lithocolletinae with the genus *Phyllonorycter* was used as a calibration point for a combined molecular phylogenetic and host plant correlation study for the genus *Phyllonorycter*. The conclusion on the sister genus dated the origin of *Phyllonorycter* to the Palaeocene (62.3 m.y.) (Lopez-Vaamonde et al. 2006; also compare Wahlberg et al. 2013).

Here, caterpillars from Upper Cretaceous Myanmar amber and Eocene Baltic amber are identified as leaf miners by typical characters (small and flat body, legs and prolegs reduced, prognathous with modified mouthparts). Caterpillars from both ambers can also be identified as putative members of the genera *Phyllonorycter* and *Phyllocnistis* and are described as new species. Their taphonomy and paleoecology is discussed.

Material and methods

Authentication of the amber inclusions is ensured by purchase from trusted salespersons and an amber inclusion collector known by long-term relations. The ambers are kept at constant temperature in plastic clip bags within metal boxes, excluding excess oxygen and light. The holotypes will be deposited at the SNSB, Bavarian State Collection of Zoology, Munich with the number SNSB-ZSM-LEP amb003 and -004. Due to the presence of pyrite the inclusions cannot be studied by micro-computer-tomography. Photographs were taken by Artur Michalski with an imaging system composed of a digital photocamera Canon EOS 4000D on a stereobinocular microscope Nikon SMZ 800, SMZ 1500 (fusion), and PLAN APO lens. For illumination, a Fiber Optical Illuminator with halogen lights was used. Image stacks were generated using COMBINE ZM software.

Results

Eocene Caterpillar from Baltic Amber

The caterpillar (Fig. 1) is a single finding, being the only specimen of its type among 1152 Lepidopteran fossils from Baltic amber in the studied collection, and of 138 caterpillars among these.

The fossil caterpillar from Baltic amber shows characteristics of leaf-mining caterpillars in being flat, small, prognathous with modified mouthparts pointing forwards, and in having reduced legs and prolegs strongly reduced or absent. Hence, it is compared to caterpillars of Lepidopteran families with leaf mining larvae, namely Acrolepiidae, Adelidae, Acanthopteroctetidae, Argyresthiidae, Bucculatricidae, Carposinidae, Choreutidae, Coleophoridae, Cosmopterygidae, Douglasiidae, Elachistidae, Eriocraniidae, Gelechiidae, Glyphipterygidae, Gracillariidae, Heliodinidae, Heliozelidae, Heterobathmiidae, Incurvariidae, Lyonetiidae, Momphidae, Nepticulidae, Palaephatidae, Prodoxidae, Pterophoridae, Pyralidae, Roeslerstammiidae, Ochsenheimeriinae, Oecophoridae, Opostegidae, Scythrididae, Tischeriidae, Tortricidae, and Yponomeutidae (Lepiforum by Csóka 2003; Hering 1951; Connor and Taverner 1997; Kristensen 1999; Pitkin et al. 2019; Ellis 2020), but also to leaf-mining families of the orders Diptera (Agromyzidae), Coleoptera (Buprestidae, Curculionidae), and Hymenoptera (Tenthredinidae) (Grimaldi and Engel 2005). Most differ in one or more of the traits body size or outlines, presence of urogomphi (Coleoptera), form of thoracic and abdominal segments, presence, or form of lateral bulges of segments, head shape, shape of last segment, and presence and kind of setae. Summarizing, the most similar caterpillars are found within Gracillariidae, especially with respect to the presence of prolegs only at A3 to A5, which is found in many Gracillariidae (pers. comm. H. Vargas 2021).

Among Gracillariidae *Phyllocnistis* (Phyllocnistinae) is close to the phenotype of the fossil caterpillar but differs in having a conical last segment and a broader thorax (Hering 1951: fig. 28; Pitkin et al. 2019 (e.g., *Phyllocnistis unipunctella*), Global Taxonomic Database of Gracillariidae, e.g., *Phyllocnistis hemera*). Phenotypes most similar or almost identical to the fossil are found from subfamily Lithocolletinae (Csóka 2003; Pitkin et al. 2019). There are twelve extant genera of Lithocolletinae, among these *Cameraria* and *Phyllonorycter* (De Prins and De Prins 2006–2021). *Cameraria* is widely known by *C. ohridella*, a prominent species as a pest of chestnut (Parenti 2000). Both genera have larvae most like the Baltic amber caterpillar, especially with respect to the triangular form of larval head (e.g., *Phyllonorycter leucographella* (Sterling and Parsons 2012)), but *C. ohridella* larvae differ in the form of the lateral bulges and the outline of the body. Most alike are larvae of *Phyllonorycter* species. Like in many Gracillariidae genera, the first larval instars (Fig. 2) are apodal and their mouthparts are modified (Parenti 2000).
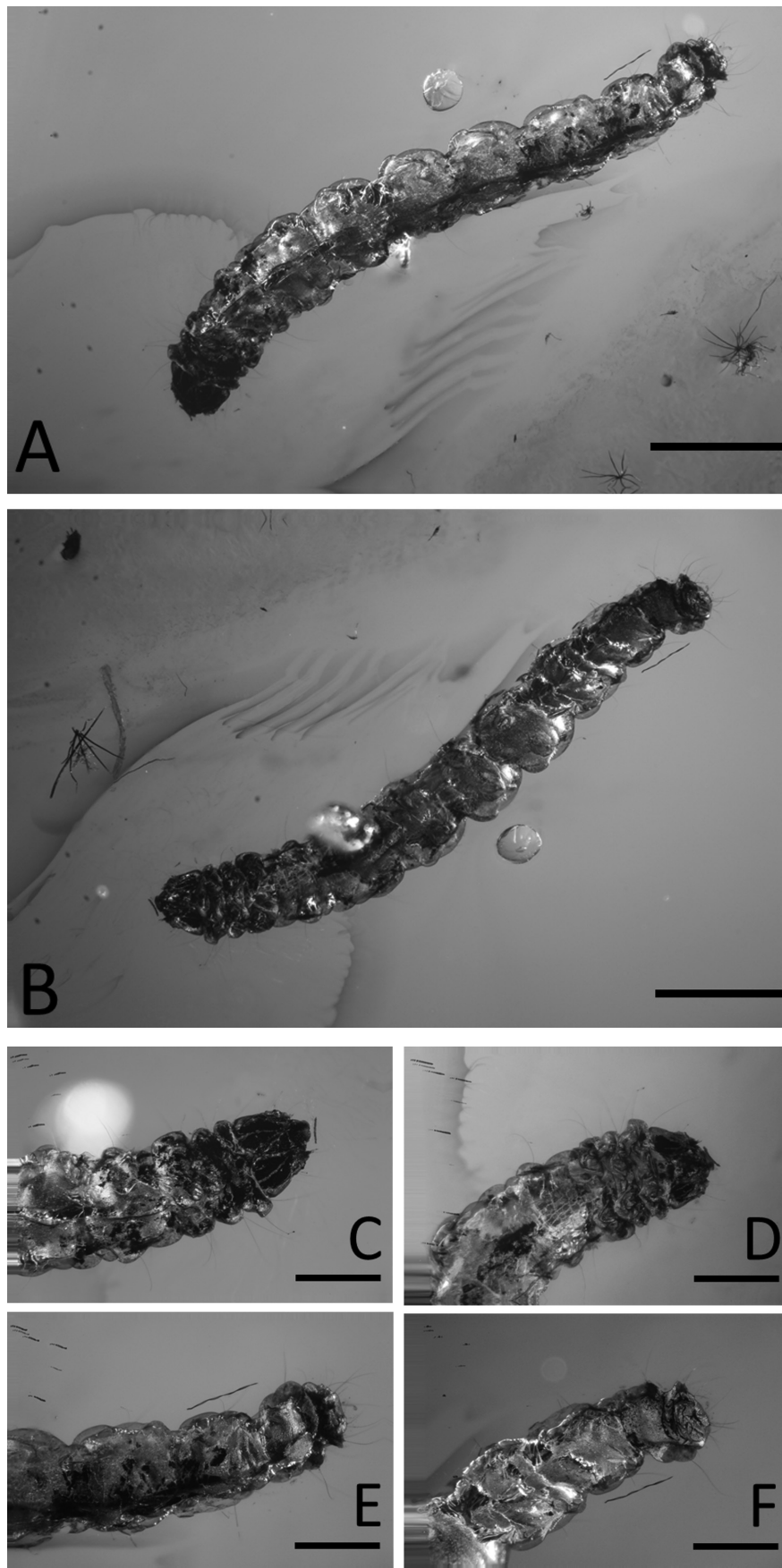
Figure 1. Holotype of *Phyllonorycter inopinata*, **A**: larva, dorsal view, **B**: ventral view, **C**: head and thoracic segments, dorsal view, **D**: ventral view, **E**: terminal segments, dorsal view, **F**: terminal segments, dorsal view. Scale bar 1 mm.

In advanced stages the larva develops thoracic legs and abdominal prolegs.

Some fossil insect taxa from Baltic amber are hard to be distinguished from their extant counterparts, e.g., *Lasius schiefferdeckeri* from extant *Lasius alienus* (or *niger* var. *alienus*) (Wilson 1955). Also, the *Phyllonorycter* caterpillar described here strongly resembles some extant species like *P. platani*. However, it is common practice not to affiliate such findings to extant species due to the lack of chance to check for internal morphologic characters or to use sequence-based approaches. Preservation of amber inclusions also may have an influence on interpretation of morphologic characters. The fossil from the Eocene of Baltic amber is consequently described as a new species of *Phyllonorycter*.

Systematic palaeontology[*]

Order Lepidoptera Linnaeus, 1758
Clade Ditrysia Börner, 1925
Superfamily Gracillarioidea Stainton, 1854
Family Gracillariidae Stainton, 1854
Genus *Phyllonorycter* Hübner, 1822

Phyllonorycter inopinata nov. spec.

http://zoobank.org/F0DEFCBA-9EAF-43EE-93C2-AD1D6E88BD5B

Etymology. The species name "*inopinata*" "surprising" refers to the seemingly unlikely find of a leaf mining caterpillar preserved in amber.

Holotypus. Specimen ex coll. Fischer no. 8182, Fig. 1
Locus typicus. Amber mine of Yantarni, RUS
Stratum typicum. "Blaue Erde" (Upper Eocene to Lower Oligocene)
Repository. Bavarian State Collection of Zoology, Munich, Germany; accession number SNSB-ZSM-LEP amb003.
Description of holotype. The caterpillar is 5 mm long and subcylindrical, maximum width 0.73 mm (in A4). The head is 0.36 mm long and 0.5 mm broad, depressed, triangular, and prognathous. Mandibles and antennae are developed. The legs are small (0,15–0.2 mm long). The thorax (T1 to T3) is 0.45 mm long and 0.63 mm broad. The longest abdominal segment is 0.61 mm (A4), the shortest abdominal segment is 0.3 mm (A9). Prolegs at abdominal segments A3 to A5 are small. There are three setae in lateral positions on either side of each segment, these are maximal 0.2 mm in length and could not be exactly positioned. The terminal segment is 0.21 mm long and 0.43 mm broad.

Diagnosis. A differential diagnosis to other *Phyllonorycter* species is currently impossible. The holotype is the only known specimen of the new species *P. inopinata*. Consequently, there is no information on variability and differences between subsequent instars. A comparison to similar extant species like *P. leucographella* or *P. platani* suffers from the same insecurities. Future findings from Baltic amber may enable a differential diagnosis.

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[*] Systematics according to van Nieukerken et al. (2011)

Cretaceous Caterpillars from Myanmar Amber

Caterpillars are rare in Myanmar amber. Only six specimens among 287 Lepidopteran inclusions from Myanmar amber are present in the studied collection, three of which are studied here.

The possibility that the larvae from Myanmar amber are non-lepidopteran was considered but can be ruled out, most obviously for the holotype of the new species with its clearly visible spinneret. Most similar in general resemblance are Buprestidae larvae (Coleoptera) which also occur in Myanmar amber (own observation). However, these have a different body outline with even thicker head and thorax, and they lack setae.

Genus *Phyllocnistis* Zeller, 1848

Species *Phyllocnistis cretacea* nov. spec.

http://zoobank.org/F0DEFCBA-9EAF-43EE-93C2-AD1D6E88BD5B

Etymology. The species name "*cretacea*" refers to the Cretaceous age of the species.

Holotypus. Specimen ex coll. Fischer no. 7513, Fig. 3.
Locus typicus. Sediments of Hukawng Valley (Myanmar).
Stratum typicum. Earliest Cenomanian, determined 99 m.y. (Cruickshank and Ko 2003; Shi et al. 2012).
Repository. Bavarian State Collection of Zoology, Munich, Germany; accession number SNSB-ZSM-LEP amb004.
Description of holotype. The caterpillar is 7 mm long and flat, maximum width 1.18 mm (in T2). The thorax (T1 to T3) is 1.06 mm long. Dorsal prothoracic plates of roughly triangular form are present (figuring alike in Hering (1951: fig. 85a). The broadest segment of the abdomen is A6 with 0.88 mm, the abdomen is 5.78 mm long. The head is 0.53 mm long and 0.75 mm broad, depressed, triangular, and prognathous. Mandibles are developed, antennae are minuscule. The spinneret is well-developed and 0.05 mm long. Legs and prolegs are not developed. The longest abdominal segment is 0.68 mm (A3), the shortest abdominal segment is 0.38 mm (A9).

There are each two lateral bulges (dorsal and ventral ones) on either side of all abdominal segments, each bulge carries a prominent seta; these setae are maximal 0.2 mm in length and bent backwards. The terminal segment is 0.28 mm long and 0.5 mm broad.

There are several syninclusions preserved in the same amber: Coleoptera (5 taxa), Hymenoptera (a wasp), Psocoptera, trichomes, a 4 mm wood fragment, arthropod feces, undefinable plant, and chitin detritus.

Description of paratype I. The caterpillar (coll. Fischer no. 7790) is 6.5 mm long and subcylindrical, maximum width 1.02 mm (in T3) (Fig. 4). The thorax (T1 to T3) is 1.25 mm long. The broadest segment of the abdomen is A4 with 0.88 mm, the abdomen is 4.41 mm long. The head is 0.39 mm long and 0.65 mm broad, depressed, triangular,
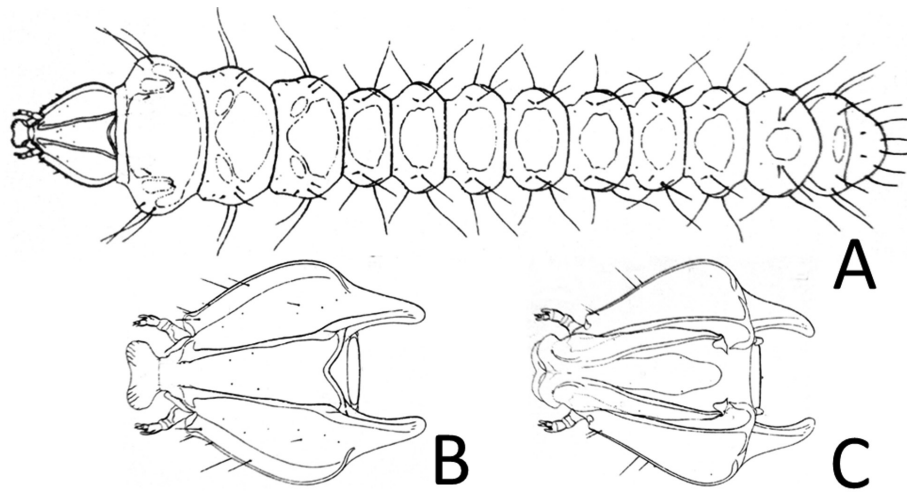
Figure 2. (changed after Parenti, 2000): First type larva (mandibles not drawn) of *Phyllonorycter platani*, **A**: larva, dorsal view, **B**: head-capsule, dorsal view, **C**: head-capsule ventral.
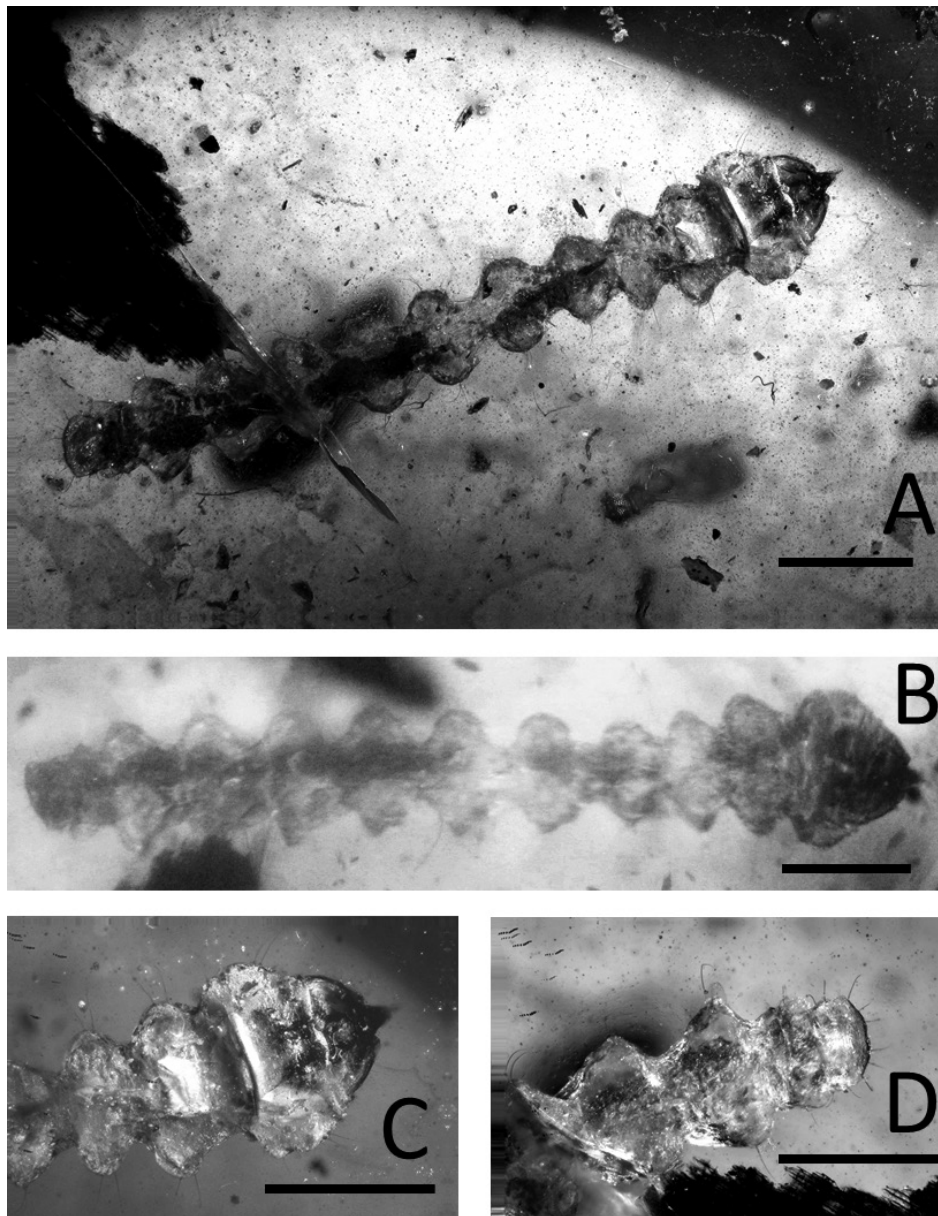

Figure 3. Holotype of *Phyllocnistis cretacea*, **A**: larva, dorsal view, **B**: ventral view (inclusion deeper within the amber), **C**: head in detail, dorsal view, **D**: terminal segments in detail, dorsal view. Scale bar: 1 mm.
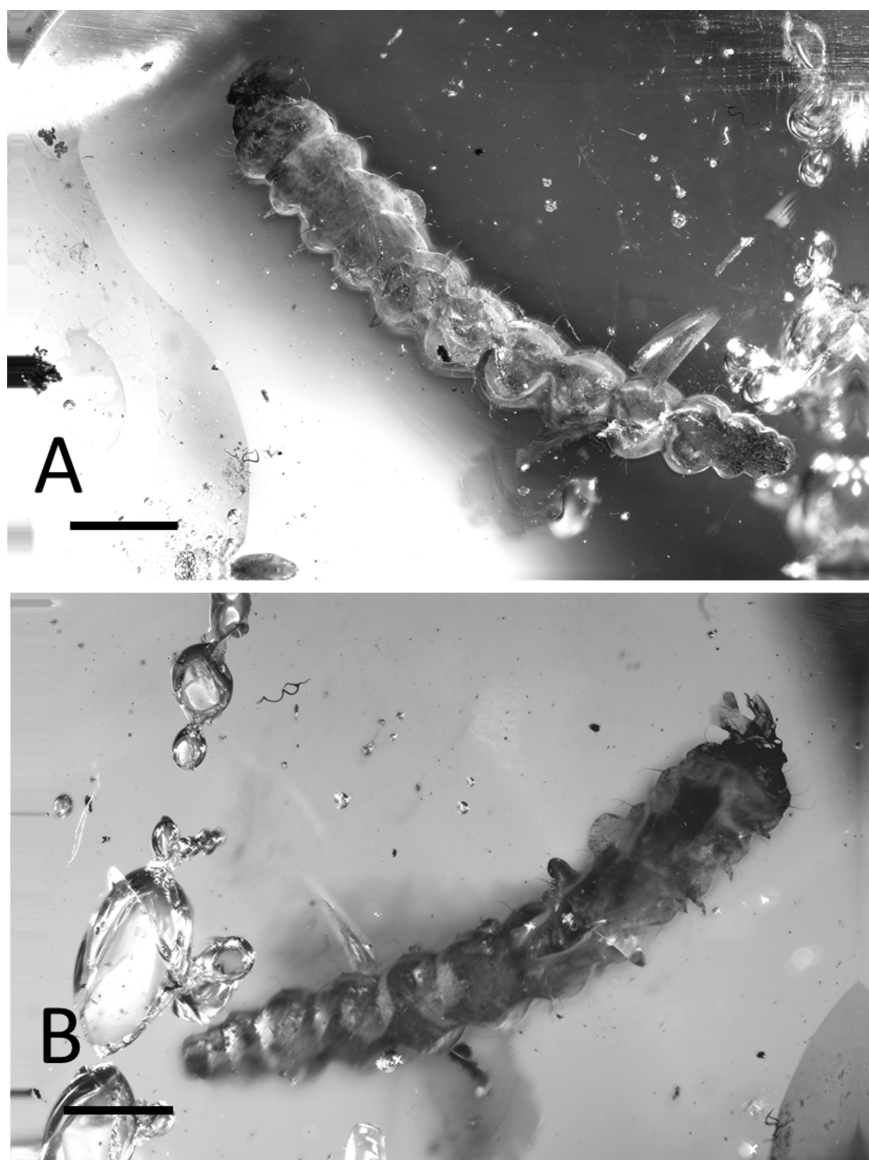
Figure 4. Paratype I of *Phyllocnistis cretacea*, **A**: larva, dorsal view, **B**: ventral view, length of caterpillar 6.5 mm. Scale bar: 1 mm.

and prognathous. Mandibles and antennae are developed. A visible leg is 0.26 mm long. The longest abdominal segment is 0.77 mm (A4), the shortest abdominal segment is 0.26 mm (A9). There are no prolegs. There are each two lateral bulges (dorsal and ventral) on either side of all abdominal segments. There are at least two setae in lateral positions on either side of each segment, these are maximal 0.16 mm in length. The terminal segment is 0.3 mm long and 0.32 mm broad.

Remark: The paratype is non-compressed, but part of the head is not well preserved. Dorsal prothoracic plates may be present, impressions with similar form are visible. A spinneret is not visible, but the head is partly hidden by some chitinous membrane.

Description of paratype II. The caterpillar (coll. Fischer no. 7512) is 4 mm long and subcylindrical, maximum width 0.83 mm (in T1) (Fig. 5). The thorax (T1 to T3) is 1.2 mm long. The broadest segment of the abdomen is A3 with 0.7 mm, the abdomen is 2.93 mm long. The head is partly retracted in the thoracic segment T1, 0.69 mm long

(visible through T1) and 0.56 mm broad, depressed, triangular, and prognathous. Head and thorax are significantly thicker than abdomen in general outline. Mandibles and antennae are developed but tiny. There are no legs and prolegs. The abdomen is 2.93 mm in length, the longest abdominal segment is 0.39 mm (A5), the shortest abdominal segment is 0.17 mm (A10). There are each two lateral bulges (dorsal and ventral) on either side of all abdominal segments. The terminal segment is 0.17 mm long and 0.3 mm broad. There are no setae visible.

Remark. There are feces preserved which were produced by the caterpillar. Some trichomes are also preserved in the amber.

Diagnosis of *Phyllocnistis cretacea*. Subcylindrical caterpillars, up to 7 mm long (in known specimens and instars), head depressed, triangular and prognathous, head partly retracted or retractable in thorax, mandibles developed, minuscule antennae present, spinneret at least in late instars present, thorax with T1 having the largest diameter of all segments, tiny legs may be devel-
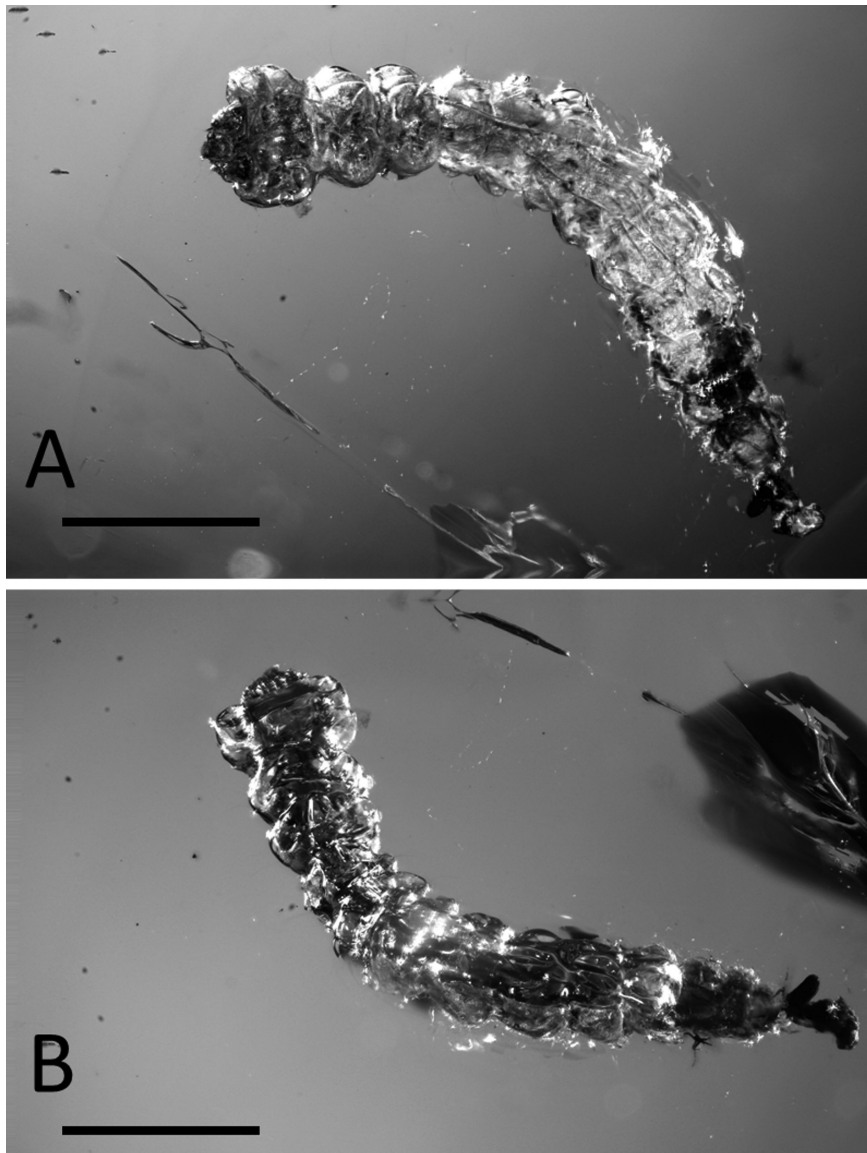
Figure 5. Paratype II of *Phyllocnistis cretacea*, **A**: larva, dorsal view, **B**: ventral view, length of caterpillar 4 mm. Scale bar: 1 mm.

oped, each segments with two lateral bulges (dorsal and ventral) on either side of all abdominal segments, setae can be present, spinneret and dorsal prothoracic plates of roughly triangular form may be developed, there are no prolegs.

Remarks. Among Lepidoptera, an affiliation to *Phyllocnistis* is affirmed by typical traits of the genus, such as having a triangular prognathous head, and lateral bulges of segments. However, the lack of prolegs casts some doubt on the identification. Most likely, at least the holotype and paratype I, but possibly also paratype II, represent late or last instars and prolegs would be expected on A3, A4 and A5 (Potts and Peterson 1960; Fracker 2015). However, the prolegs may be too tiny to be detectable with respect to the preservation state. It is assumed here that reduction of proleg development for some larval stages could occur at species level as reduction of legs and prolegs is common in mining Lepidoptera (Hering, 1951). Future finds of such caterpillars hopefully will allow to differentiate larval stages or related species.

Discussion

Leaf mining habit and identification

The prognathous mouthparts of the caterpillars are the most evident character for feeding by mining. The function of such mouthparts can be illustrated by a microscopic video (https://www.youtube.com/watch?v=LqL6LKEg-05k&feature=youtu.be). The characteristic lateral bulges present at every segment are especially well developed in many species of the leaf-mining genus *Phyllonorycter*, but also in some quite unrelated miners like leaf-mining Buprestidae (Coleoptera) larvae (Csóka 2003: 168; Grimaldi and Engel 2005). They may be due to convergent evolution with maximisation of body mass keeping good lateral flexibility of the abdomen. Other traits characteristic for miners (flat, small, legs and prolegs reduced) are also present in the studied amber inclusions. However, the caterpillars are relatively large for miners, are only subcylindrical and have somewhat developed legs. In *Phyllonorycter* prolegs

are present in the final instars (Scoble 2002: 116). Prolegs are absent in early instars of Gracillariidae (Scoble 2002: 116). The change from small apodal and flat early instars is described for later instars of Lithocolletinae (and other Gracillariidae) and termed hypermetamorphosis, and there may be even more stages like in *Marmara arbutiella* (Wagner et al. 2000). The fossil *Phyllonorycter* caterpillar described here may represent the third to fifth instar, referring to description of extant larval development in Lithocolletinae (Fracker 1915; Davis and Robinson 1998; Parenti 2000). Fracker (1915) mentions the character "prolegs at A3 to A5" (not A6) as a distinctive feature of later instars of (extant) Gracillariidae in general. The presence of mandibles (also in the *Phyllocnistis* caterpillars from Myanmar amber) argues against interpretation as last instars.

The phenotype of the specimen from Baltic amber allows a putative identification as *Phyllonorycter* (Gracillariidae) as described above. The finding is a direct evidence for the genus, subfamily and family and validates the evidence for the presence of the taxa by fossil mines (citations given in Introduction).

The specimens from Myanmar amber are similar regarding general phenotype but differ in a thicker thorax and a partly retracted or retractable head. This phenotype is found in extant *Phyllocnistis* (Gracillariidae) and some of the larval stages of *Spinivalva gaucha*, a neotropical Gracillariinae taxon (Brito et al. 2013). *Dendrorycter marmaroides* Kumata 1978 is similar with respect to the presence of two lateral bulges (dorsal and ventral), but these are pointing backwards. *Phyllocnistis* has a small spinneret (Cerdeña et al. 2020; pers. comm. H. Vargas 2021), in contrast in the Cretaceous holotype the spinneret is well developed. The interpretation of a size reduction of the spinneret as the derived state with the extant genus seems to be realistic.

Gracillariidae are basal Ditrysia which retained the primitive larval feeding and live mode by mining found in many basal Lepidoptera except the most basal families like detrivorous Micropterigidae (Menken et al. 2009). Exclusively internal feeding gives protection from predators, weather, desiccation, UV-radiation, and assures a reliable food supply. Leaf mining puts a constraint on body size of the larva and often goes along with monophagy and host dependence (Connor and Taverner 1997; Csóka 2003). However, in Gracillariidae hypermetamorphosis occurs in late larval instars and may be accompanied by a switch to external feeding, change of mine and leaf (Hering 1951), or may allow external pupation (Parenti 2000). Gracillariidae are mainly hosted by Eurosids I (Menken et al. 2009), a broad group of angiosperm families. Nevertheless, monophagy is realized by numerous species of *Phyllonorycter* which use specific plant genera or species as hosts (e.g., Pitkin et al. 2019).

Eocene *Phyllonorycter inopinata* caterpillar from Baltic Amber

Extant *Phyllonorycter* species mine on oaks and beech (*Quercus, Fagus,* Fagaceae), birch (*Betula*), hornbeams (*Carpinus, Ostrya*), alder (*Alnus*, all Betulaceae), hazel (*Corylus*, Corylaceae), hawthorne (*Crataegus*), apple (*Malus*), pear (*Pyrus*), quince and medlar (*Cydonia / Chaenomeles*), snowy Mespilus (*Mespilus*), wild service tree (*Amelanchier*) and rowan (*Sorbus*), cherry, plum and blackthorn (*Prunus*), pyracanth (*Pyracantha*), cotoneaster (Cotoneaster) (all Rosaceae), willow (*Salix*), poplar (*Populus*) (both Salicaceae), honeysuckles (*Lonicera, Leycesteria*), snowberry (*Symphoricarpus*), arrowwood (*Viburnum*, all Caprifoliaceae), sycamore (*Acer*, Aceraceae), plane (*Platanus*, Platanaceae), elm tree (*Ulmus*, Ulmaceae), cowberry (*Vaccinium*, Ericaceae), broom (*Cytisus*, *Genista*), greenweed (*Chamaecytisus*), laburnum (*Laburnum*) and gorse (*Ulex*, all Fabaceae) and various clovers and beans (*Trifolium*, *Vicia* and other herbaceous Fabaceae), scabious (*Scabiosa*, Dipsacaceae, herbaceous), and especially stressed plants (Csóka 2003; Pitkin et al. 2019). Most important host for *Phyllonorycter* seem oaks, Betulaceae, Rosaceae and Salicaceae. Arborescent plants are preferred rather than herbaceous ones, and only dicotyledonous plants in general.

Among the group of extant *Phyllonorycter* host genera, there is fossil evidence from Baltic amber for the presence of *Quercus*, *Fagus* (Fagaceae, but also other genera are known), *Alnus*, *Betula*, *Carpinus* (Betulaceae), *Corylus* (Corylaceae), Rosaceae indet., "*Populitis*", *Salix* (Salicaceae), *Acer* (Aceraceae), *Ulmus* (Ulmaceae), and Ericaceae indet.

Oaks must have been widely distributed in Baltic amber forest, as stellate trichomes of oaks are by far the most abundant plant remains in Baltic amber, occurring in about every second piece. Male oak inflorescences are also well known, and many species of *Quercus* have been described from Baltic amber (Spahr 1993; Gröhn and Kobbert 2017). Hence, oaks seem possible hosts for *Phyllonorycter* in the Baltic amber forest.

However, the climate in Eocene Baltic amber has been tropical (e.g., Grimaldi and Engel 2005). This contrasts with extant *Phyllonorycter* hosts described mostly from temperate regions, but many plant genera are known from Baltic amber which nowadays do occur in subtropical climates (e.g., Magnoliaceae, Dilleniaceae (Spahr 1993)). Hence, there is uncertainty in considerations on putative host plants for the fossil miner.

Pupation of *Phyllonorycter* is reported to normally occur within their blotch mines (Davis and Robinson 1998), giving a possible explanation for the rarity of the find of a later instar caterpillar in a fossil resin like Baltic amber (and Myanmar amber, see below). However, the closely related taxon *Anarsioses aberrans* exits the mine for pupation and has been differentiated from its former affiliation *Phyllonorycter aberrans* (Braun) for this behaviour and some differences in male genitalia (the latter without fossilization potential) (Davis 2019).

The descriptions of *Gracillariites lithuanicus* and *G. mixtus* (Kozlov 1987) are scarce, and the imagos seem to be too undersized to become correlated with the caterpillar taxon *Phyllonorycter inopinata*.

Upper Cretaceous caterpillar *Phyllocnistis cretacea* from Myanmar Amber

The origin of *Phyllonorycter* had been dated back at least to the Palaeocene (62.3 m.y.) by molecular phylogenetic analysis using mines of the sister taxon *Phyllocnistis* for calibration of divergence (Lopez-Vaamonde et al. 2006). The findings from Myanmar amber which is dated to 99 m.y. (Shi et al. 2012) and the putative identification as *Phyllocnistis* predate the occurrence of the genus and place its origin closer to the radiation of their angiospermous host plants.

Little is known about the flora and putative host plants from the biotope in which Myanmar amber originated. The origin of the resin is suggested to be the Cupressaceae conifer *Metasequoia* (Grimaldi et al. 2002) or an araucarian pine (Poinar et al. 2007). The environment was reported to be tropical (Grimaldi et al. 2002); botanical fossils are found but have remained mostly unstudied.

Mode of living and taphonomy

An interesting question is the evolution of hypermetamorphosis of late stages in larval development of Gracillariidae and its relation to larval size and internal versus external feeding, change of mine and host leaf, and the place of pupation.

Leaf miners seem to have little potential in fossilization as caterpillars would have to leave or get exposed from their mines to become embedded in resin for subsequent fossilization. Up to now only mines in fossil leaves had been known.

The fossil caterpillars described here possibly either have left their mines for external feeding or, more likely with respect to their prognathous mouthparts and the well-developed spinneret, for outside pupation. For extant Gracillariidae both, pupation inside the mine or derived structures (ptychonomes) or outside of the mine, is known (Parenti 2000). Alternatively, the caterpillars preserved in amber were driven out of their mines by resin flow, drying of the leaf or some other mechanical force breaking the mine. From the collection under study there is an inclusion in Baltic amber of an early instar of a Psychidae – Typhoniinae larva obviously driven out from its still intact case by resin flow and found close to this case (not shown). This finding demonstrates that this embedding effect may occur as early instar Psychidae larvae (to the best of the author's knowledge) do not leave their cases.

The presence of a well-developed spinneret and the presence of legs seem to strengthen the hypothesis that caterpillars left their mines for pupation. External feeding usually is accompanied with hypognathous (pointing downwards) mouthparts, sitting on a leaf or other plant organ, and feeding below it and at an edge. External feeding seems unlikely for the caterpillars described here due to their prognathous mouthparts in combination with a well-developed spinneret. Hering (1951) states that prog-

nathous Gracillariidae larvae die when they are removed from their mines. Given this interpretation, a driving force for hypermetamorphosis with late development of legs (and prolegs in *P. inopinata*) could be the ability to search for better places for pupation. For sure, this conclusion is hypothetical and needs confirmation by other further findings or support from other lines of evidence.

Conclusions

The finding from the Upper Cretaceous gives direct evidence of leaf-mining caterpillars, beyond their known fossil mines. Minimal geological ages for the proposed identifications *Phyllonorycter* and *Phyllocnistis* could be concluded, with the insecurities discussed. Both findings confirm the conservative character of the leaf-mining habit for well-known extant leaf-miner taxa. There is now some more evidence for the hypothesis that evolution of hypermetamorphosis in Gracillariidae might have been driven by facilitating pupation outside the leaf mine.

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Mandatory statement

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