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A revised checklist of Nepticulidae fossils (Lepidoptera) indicates an Early Cretaceous origin

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Abstract

With phylogenetic knowledge of Lepidoptera rapidly increasing, catalysed by increasingly powerful molecular techniques, the demand for fossil calibration points to estimate an evolutionary timeframe for the order is becoming an increasingly pressing issue. The family Nepticulidae is a species rich, basal branch within the phylogeny of the Lepidoptera, characterized by larval leaf-mining habits, and thereby represents a potentially important lineage whose evolutionary history can be established more thoroughly with the potential use of fossil calibration points. Using our experience with extant global Nepticulidae, we discuss a list of characters that may be used to assign fossil leaf mines to Nepticulidae, and suggest useful methods for classifying relevant fossil material. We present a checklist of 79 records of Nepticulidae representing adult and leaf-mine fossils mentioned in literature, often with multiple exemplars constituting a single record. We provide our interpretation of these fossils. Two species now are included in the collective generic name *Stigmellites*: *Stigmellites resupinata* (Krassilov, 2008) comb. nov. (from *Ophiheliconoma*) and *Stigmellites almeidae* (Martins-Neto, 1989) comb. nov. (from *Nepticula*). Eleven records are for the first time attributed to Nepticulidae. After discarding several dubious records, including one possibly placing the family at a latest Jurassic position, we conclude that the oldest fossils likely attributable to Nepticulidae are several exemplars representing a variety of species from the Dakota Formation (USA). The relevant strata containing these earliest fossils are now dated at 102 Ma (million years ago) in age, corresponding to the latest Albian Stage of the Early Cretaceous. Integration of all records in the checklist shows that a continuous presence of nepticulid-like leaf mines preserved as compression–impression fossils and by amber entombment of adults have a fossil record extending to the latest Early Cretaceous.

Key words: Baltic Amber, Calibration points, Dakota Formation, Evolutionary history, Extinction, Fossil record, Larvae, Leaf mining, Plant hosts, *Stigmella*, *Stigmellites*

Introduction

Numerous molecular phylogenetic studies spanning the entire megadiverse insect order Lepidoptera have been published during the past five years (Mutanen *et al.* 2010; Regier *et al.* 2009; Regier *et al.* 2013; Timmermans *et al.* 2014). Although there is as yet no complete consensus for all phylogenetic relationships, especially among superfamilies (Timmermans *et al.* 2014), the overall topology for the evolution of Lepidoptera presently is clearer than ever. This advancement offers opportunities to study the timeframe during which their evolution took place. One recent study used seven fossil calibration points across all Lepidoptera and has revealed several periods of increased diversification and a plausible, synchronous evolution with angiosperm hosts (Wahlberg *et al.* 2013). Their work became possible by combining the Mutanen *et al.* (2010) phylogenetic dataset with a LepTree project compilation of fossils (Sohn *et al.* 2012; Sohn & Lamas 2013). Molecular dating on phylogenetic trees has been a subject of considerable scientific debate, ranging from pointing out the pitfalls of using poorly supported

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phylogenetic trees as starting points, to the sensitivity of different Bayesian priors such as mutation rates, the amount of data partitions, or the effects of modelling calibration priors (Wheat & Wahlberg 2013). When such technical issues are taken into account, the remaining, most important factor in constructing a timed phylogenetic tree is the number and reliability of calibration points, including the issue of establishing additional dates (Magallón *et al.* 2013). The reliability of these dates are assured only when such age dates can be assigned to a particular phylogenetic node with a high degree of certainty. In summary, calibration points require reliable identifications.

Nepticulidae commonly are known as pygmy moths and constitute a species rich, basal family within lepidopteran phylogeny, and consequently may offer a series of calibration points of both practical and theoretical importance (see Regier *et al.* 2015). The family comprises some of the smallest adult Lepidoptera known, and is found on all continents except Antarctica. All nepticulid species are herbivores with larvae that feed inside host-plant tissues. There are a variety of larval feeding modes within the family, including gall-formers, fruit-miners, bud-miners, stem-miners and bark-miners, but the vast majority of species are leaf miners. The identification of extant species from larval leaf-mining traces often is reliable, although somewhat dependent on geographic region and highly contingent on correct host identification. Many species are (strict) monophages or oligophages (sensu Menken & Roessingh 1998), and some genera or species groups are specialized on a single plant family. Several studies provide a phylogeny of the family or its subgroups (Scoble 1983, van Nieukerken 1986, Puplesis 1994, Hoare & van Nieukerken 2013, Doorenweerd *et al.* 2015).

Fossils of adult Lepidoptera are rare, but recently fossils of leaf mines frequently have been encountered (Labandeira *et al.* 1994; Sohn *et al.* 2012; Donovan *et al.* 2014). However, identifying leaf-mining taxa from traces, or larval mediated damage on fossilized leaves requires an alternative approach, when compared to the identification of extant species. The difference in approaches is that there is no independent knowledge of the biogeographical distribution or plant-host specificities of the fossil taxa. In addition, the characters that leaf mines provide are largely behavioural, and because they are influenced by environmental conditions, they also are prone to homoplasy.

It is relatively easy to distinguish a fossil leaf mine from other types of biotic and abiotic foliar damage by focusing on those features that also are relevant for identification. The presence of wound reaction tissue that surrounds oviposition sites is indicative of miner insertion of eggs into inner leaf tissues. The colour and differential contrast in hues among the surrounding leaf tissue, the mine trajectory and mine's contents also provide additional information. The mined areas are thinner and thus paler and of lighter hue than surrounding unaffected tissue, whereas a frass trail consists of concentrated faecal contents and will be darker in hue. Distinguishing between miners feeding on parenchyma and sap-feeding miners consuming epidermal tissues also is important. Sap feeding occurs among extant groups only in several early instar larvae of Gracillariidae and some Agromyzidae (Diptera) (Winkler *et al.* 2010). Only larvae of Phyllocnistinae and Oecophyllembiinae (Gracillariidae) are sap feeding throughout their entire larval feeding period (Davis & Robinson 1998; Hering 1951; Kumata 1998). Parenchyma feeding leaf miners are more common and are found in four insect orders: Diptera, Hymenoptera, Coleoptera and Lepidoptera. Leaf mining is overwhelmingly the most common type of plant mining damage encountered in the fossil record, and, of the different mining types, it provides the most characters for taxonomic identification. A focus on those combinations of characters of taxonomic relevance could result in the identification of a fossil leaf-mine specimen at least to the family level.

Body fossils of adult Nepticulidae are exceedingly scarce, but constitute the most valuable candidates for calibrating genus-level nodes in phylogenies. If sufficient characters are visible, identifications to genus or even species groups are possible. There are 13 adult fossils that have been assigned to Nepticulidae in the literature, some of which have tentative affiliations. Two of these occurrences are compression–impression fossils from the Late Priabonian (Late Eocene) and provide partly visible wing venation. Two others are found in resin-like copal and likely are not older than 150,000 years (Labandeira *et al.* 1994). Seven adult fossils originate from Baltic Amber. Another candidate specimen originates from mid Late Cretaceous Canadian Amber, and an additional specimen lacks a clear stratigraphic provenance. Adult fossils from Baltic Amber are dated from 44.4 to 33.9 Ma, and their occurrences reflect multiple phases of sedimentary recycling of original older amber into successively more recent deposits (Labandeira 2014). The Canadian Amber specimen is estimated to be 72 Ma.

Earlier reviews of Lepidoptera fossils that list Nepticulidae include Skalski (1990a) and Sohn *et al.* (2012), but here we present the most comprehensive and revised checklist to date. Five amber fossils have been described since the latest review in 2012, more than doubling the number of known nepticulid amber fossils (Fischer 2013). Nepticulidae form a Superfamily, Nepticuloidea, together with the Opostegidae, of which the latter lack known fossils. Opostegidae also are herbivores, but, to the extent that larval habits are known, the majority of extant species create stem- or bark-mines, often consuming cambium tissue; very few species construct mines in leaves (Regier *et al.* 2015). Larval traces of mines in bark or cambium are difficult to find and recognize, even in modern live hosts, and the absence of their traces in the fossil record is not surprising. Given the absence of opostegid fossils, the checklist presented here can also be viewed as a checklist for the Superfamily Nepticuloidea. The list is constructed in such a way that it maximizes the potential in calibrating nodes for molecular dating analyses of Nepticulidae, related lineages, and Lepidoptera at large.

Material and methods

Identifying fossil adult Nepticulidae. Identification of fossil adult Nepticulidae relies on the same characters that distinguish extant species (e.g. Johansson *et al.* 1990, van Nieukerken 1986), although commonly only a subset of those characters are preserved or evident in the fossil record. The family as a whole may be tentatively recognized by a combination of their small size; the presence of an enlarged first antennal segment (scape), also known as the eye-cap; erect hair-like scales on the frons and vertex of the head (the frontal tuft); the presence of maxillary and labial palps; usually a short haustellum; and relatively short legs, without a tibial epiphysis. An additional combination of external characters, particularly wing venational features, may lead to a genus level identification. As with many groups of insects, genitalia are the most reliable source of characters for species-level identification. Most amber inclusions of adults, however, are internally hollow, a phenomenon that results from the degradation of internal organs (Labandeira 2014), and genitalia may be absent or partially preserved.

Identifying Nepticulidae from fossil leaf mines. Identification of fossil leaf mines is less exact than identification of adults, mostly because the characters of leaf mines have never been analysed in a phylogenetic context. For many taxa there is a combination of characters that distinguishes the group, but for each individual character there usually are exceptions that obstruct the designation of truly synapomorphic characters. Moreover, many characters are difficult to describe in a quantitative manner, such as the shape of the mine or distribution of faecal pellets (microcoprolites) within the mine's frass trail. In practice, the identifications depend on cumulative evidence. Below, we describe the relevant characters that we have evaluated.

Oviposition. Nepticulidae oviposit on the exposed surfaces of plant tissue, and consequently, there is no scarring around the oviposition site. Female Nepticulidae deposit an egg-case that covers the entire egg. The egg-case materials consist of a secretion from the collaterial glands resulting in a shiny speck, which typically is black when the larva has hatched (van Nieukerken *et al.* 1990, figures on page 31). However, this structure is lost relatively easily with post-mortem plant-tissue decay, and may be more difficult to recover or recognize in fossils. Notably, an egg case may also be observed in mines made by the genus *Leucoptera* (Lepidoptera: Lyonetiidae), or alternatively coleopteran leaf-mining groups, such as the genus *Trachys* (Buprestidae) (Ellis 2014; Emmet 1988; Ding *et al.,* 2014).

Leaf-mine shape. The shape of the mine is the feature that is of most immediate concern for the description and classification of leaf-mine records. Leaf-mine shape usually constitutes the most conspicuous set of characters. Nepticulidae leaf mines are highly variable, and include linear galleries, blotches or a combination of a gallery and a blotch (see text box "Leaf-mine terminology" and Figs 1–9). Much of this structural variation is present in the most species rich, extant genus, *Stigmella* (Figs 2, 4, 9). Therefore, it is not surprising that most fossil records mention a resemblance to species of extant *Stigmella*. Nevertheless, several other extant genera contain very similar mine types, particularly as the linear mine very commonly occurs in the genera *Acalyptris* (Fig. 1), *Enteucha, Roscidotoga* (Fig. 6)*, Pectinivalva* and *Parafomoria*. The second largest genus in the family, *Ectoedemia*, has leaf mines that typically, but not always, start as a thin, usually strongly meandering, gallery mine that abruptly change into a broad blotch, termed an ophistigmatonome (Figs 3, 8). Several fossil mines display an analogy to this mine type, such as *Stigmellites samsonovi* Kozlov, 1988 or *Ectoedemia* sp. (Labandeira *et al.* 1994) (Fig. 18), but such a sequence of mine phases is not an apomorphic trait within the family, and occurs also in other genera (for example, Figs 7, 9 with *Bohemannia* and *Stigmella*, respectively). Nepticulidae larvae generally avoid veins, as they rarely cross primary or otherwise prominent veins, such as midribs of dicotyledonous angiosperms;

only later instar larvae have the ability to cross secondary veins. Another relevant feature is the total length of the mine, which from oviposition site to emergence area can range from very short in small mines, likely attributable to early instar Bucculatricidae or Coleoptera that later feed externally, to very long linear mines or large blister-like mines that are more likely made by Lyonetiidae, Gracillariidae, Eriocraniidae, Hymenoptera or some Coleoptera. Care should be taken to only judge the length of completed mines, which may be recognized by the lack of frass at the emergence area. Incomplete mines may contain perished, possibly parasitized, larval remains, particularly mandibles and head capsules. Backtracking, or reversing the larval trajectory of a mined route, combined with initiating a new mining direction, is very rare in Nepticulidae. However, backtracking without starting a new trajectory occasionally occurs, evident from frass trails occurring on both sides of a mine, resulting in a central, frass-free path. Such a condition is seen, for example, in the *Ectoedemia populella* group where larvae retreat into the petiole or midrib during the day. Leaf-mining shapes with backtracking and changes of direction are more typical for *Parectopa* (Gracillariidae) or *Cosmopterix* (Cosmopterigidae), but also occur commonly in many dipteran (Winkler *et al*. 2010) and coleopteran (Ding *et al*. 2014) leaf mines.

Frass. The frass of Nepticulidae consists of granular pellets that are deposited often in a species-specific mode, but do not constitute a distinct, synapomorphic pattern that follows from the movements of the larva in the mine. The range of frass patterns include a central or laterally positioned, thin frass line (Fig. 5), randomly distributed pellets filling the width of the mine (Fig. 6); frass deposited in meniscate arcs (Fig. 2); or distinctive, abrupt changes in the frass pattern following each moult. Some species spread the frass in the final instar along two lateral lines and move in between these trails, examples of which are the *Ectoedemia populella* group (Johansson *et a*l. 1990, Ellis 2014: *e.g.* http://www.bladmineerders.nl/minersf/lepidopteramin/ectoedemia/intimella/intimella.htm), or the oak miners *Stigmella kao* van Nieukerken & Liu and *S. lithocarpella* van Nieukerken & Liu (van Nieukerken and Liu 2000, Figs 95, 96, or http://nepticuloidea.info/stigmella-kao-13; http://nepticuloidea.info/stigmella-lithocarpella-7). In Diptera, frass is generally more fluidized, consists of fewer pellets, and often is deposited in a double-track manner, owing to the larva residing laterally, on its side, within the mine, or occasionally is not visible (Winkler *et al.* 2010). Hymenopteran frass is often arranged into threads or elongate pellets and occasionally is actively removed by the larva from the mine. Coleopteran frass usually comprises granular pellets, or strings of pellets, or elongate pellets (Ding *et al.* 2014). Leaf mines on non-woody herbaceous plants are more commonly made by dipteran leaf miners than any other order of leaf miners (Spencer 1990), although when Lepidoptera, including Nepticulidae, do mine herbaceous plants, they tend to have a more fluidised, dipteran-like frass as well (Fig. 8). The presence, shape, and depositional pattern of the frass within the mine are important characters. Occasionally, the pattern may change abruptly after moulting, and careful examination of the mine may reveal exuviae of earlier moults, including head capsules.

Larva. None of the published fossil records include fossilized larvae. If larvae are present, however, they would provide an important source of characters. Features of the chitinous head capsule frequently are diagnostic to order, usually to family and possibly even to genus, when clearly visible (for Nepticulidae, see Gustafsson & van Nieukerken 1990). Other characters of the larva, such as the presence or reduction of legs and prolegs and the constriction between segments also are informative. Nepticulidae never have prolegs or thoracic legs, and the body is minimally constricted between adjacent segments.

Pupation. Numerous publications claiming to present fossil nepticulid mines mention a "pupation chamber" at the final section or terminus of the mine (e.g. Stephenson 1991), or indicate that the presence of a semi-circular slit at the end of the mine is a reliable character for distinguishing dipteran from lepidopteran mines. With the exception of some species of *Ectoedemia* and *Trifurcula*, all Nepticulidae pupate outside the mine. They create a semi-circular slit to exit the mine (clearly visible in Fig. 7), similar to many Diptera, and usually descend to the soil on a silken thread where they pupate within a silken cocoon. A related feature is the final section of the mine, which is devoid of frass, as the mine terminus is where the larva resides before vacating the mine. The absence of frass at the mine terminus may be used to indicate the final size of the larva, but should not be interpreted as a pupation chamber. In such mines there are never traces of silk, but some species that do pupate in the mine may construct a cocoon within a silken tunnel that is connected to a previously made slit in the epidermis. Larvae that make such structures include species in the subgenus *Ectoedemia* (*Fomoria*) (Johansson *et al.* 1990) (Fig. 8).

Plant hosts. Identification of the plant host is a crucial step when identifying extant species from leaf mines. However, plant hosts from the fossil record should be viewed in a different perspective. It is likely that many fossil leaf-mining species are extinct, and modern taxa may have recolonized ancient hosts, or that new hosts may have been colonized (Labandeira 2002b). The identification of fossil leaves frequently is not straightforward, and assignment to a certain plant family may be incorrect, especially in treatments from the older literature. With modern and more detailed methods, many plant-host identifications of the older literature subsequently have been revised, and in many cases it is impossible to assign fossil leaves to any particular, modern taxonomic group. One example is the assignments to Proteaceae listed by Berry (1916), of which none probably belong to that family (Dilcher 1973). Dilcher comments that "Many early Tertiary, and certainly many Cretaceous, fossil angiosperm leaves should not be expected to have characters that relate them at the generic level with modern forms." Recently, there has been the tendency to erect extinct genera and families for groups of angiosperm species that are extinct and are devoid of extant representatives (Friis *et al.* 2011). A more practical approach is use of a foliage morphotype system (Johnson 2002) to be followed by an upgrading to a Linnaean binomial once leaf morphology and variation has been extensively documented (Johnson, 1996). We have endeavoured to place the fossil hosts into their families and provide author names using several online sources (including http://fossilworks.org/ and http://www.theplantlist.org/ for extant plants), but we have not ascertained whether all names are valid.

Some generalizations regarding nepticuloid patterns of host-plant occurrence may be useful to mention. All Nepticulidae feed on angiosperms, mostly on eudicots, except for a few species within *Stigmella* that feed on Poaceae or Cyperaceae. As well, some *Acalyptris* species feed on Cyperaceae and an unclassified species from Brazil has mines found on *Piper* (Piperaceae, Magnoliales) (Kemperman *et al.* 1985; Wilkinson 1979; van Nieukerken, unpublished data). In general, lepidopterous leaf mines on commelinid monocots are more likely created by Elachistidae (Kaila 2011). The nepticulid genus *Roscidotoga* is specialized on Oxalidales and is restricted to Australia (van Nieukerken *et al.* 2011a), although a few other Oxalidales feeders are known outside Australia (EJvN, unpublished data). Most species of the genus *Enteucha* are found on Polygonaceae (van Nieukerken 1986); only one other nepticulid is known to feed on this plant family, an unnamed species of *Acalyptris* that feeds on *Eriogonum* (D.L. Wagner, personal communication). Only species from the genus *Parafomoria* and a species of *Stigmella*, *S. diniensis* (Klimesch), feed on Cistaceae (Sapindales) (van Nieukerken 1983).

Revision of published records. We reviewed the literature on fossils of Nepticuloidea and documented all references to fossils that have been assigned to Nepticuloidea. Where possible, we re-evaluated the characters used for specimen identification from images or drawings, and when available, the original photographs and amber fossils were obtained on loan for further study. When judging the identifications for material not in our possession, we were aware that the original authors probably had a better view of the material than we have from published images. Many of the records received new identifications based on our collective experience and insight. For records that could not be verified, we judged whether the assigned rank was plausible in terms of geological age and the characters described in the text. If they were plausible, we did not change the identification, but these records have their identification denoted with "[unverifiable]". Uncertain attribution to the identified rank is indicated with cf. (Latin: compare). In general, we were reluctant to assign an extant, genus-level rank to a leaf-mine fossil; most are ranked under Nepticulidae *incertae sedis* or are placed in the ichnogenus *Stigmellites*. The only exceptions allowed were for subfossil leaf mines that resemble more recent extant species, such as *Stigmella ulmivora* (Fologne) (record #14), or mines from host plants and regions where we see a continuous record between the Neogene fauna and the present fauna—for example: *Stigmella* on Californian oaks—in which mines closely resemble extant ones (Opler 1973). Several original descriptions and translations, and when possible, illustrations are placed on the website Nepticuloidea.info (van Nieukerken 2014). We reviewed 79 fossil records, of which many contain multiple exemplars. One correction for several records involved a preservationally exceptional deposit, or Lagerstätte, for Neogene leaf fossils, Willershausen am Harz, in Germany. This deposit was confused by Sohn *et al.* (2012) with another Willershausen locality in the federal state of Hesse (Hessen), which resulted in the confounding addition of the state of Brandenburg. Instead, fossil Lagerstätte of Willershausen am Harz is located in the state of Niedersachsen (Lower Saxony), and belongs to the municipality (Gemeinde) of Kalefeld, in the District (Landkreis) of Northeim (N51.7845° E10.1087°).

Each unique combination of geologic stage, locality, host and identification is given a record number. A single record can include multiple exemplars or undescribed taxa. We treat the fossils in the checklist by preservational type and by age: first the adults from the oldest to recent, and then the compressions or impressions of leaf-mines on fossil foliage from oldest to recent. We have numbered the fossil records and present details for each fossil in the following format:

- # Record number *Genus species* author. This is the revised identification.

A chronological list of previous identifications and publications.

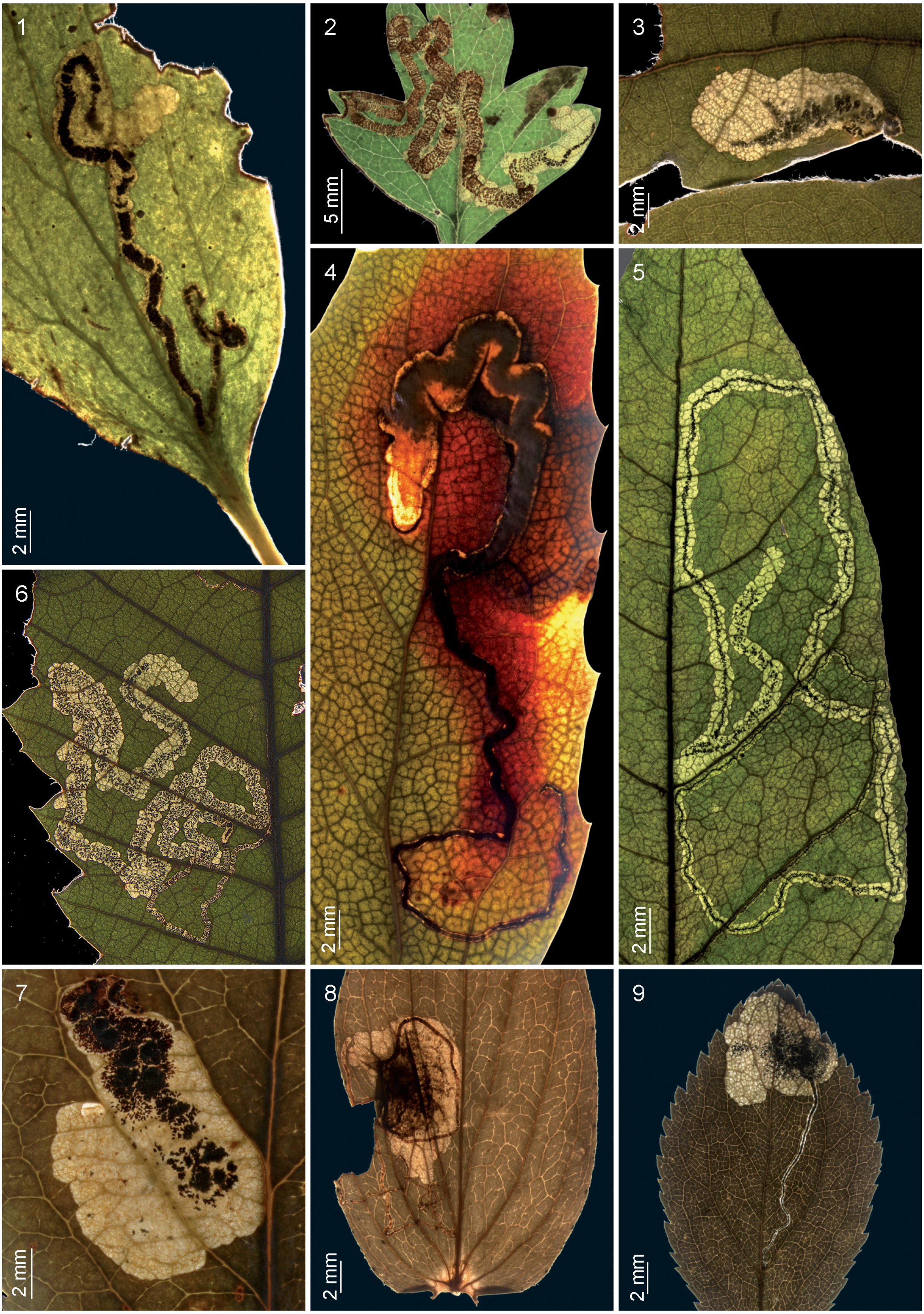
- fossil type—Host: host plant—[number of exemplars] Coll: collection
- Loc: the fossil locality
- Stratum: the fossil deposit
- Remarks: revisionary comments and observations

Alphabetical list of collections abbreviations

BMNH	Department of Paleontology, Natural History Museum, London, United Kingdom
BPGM	Bavarian State Collection for Paleontology and Geology (= Bayerische Staatssammlung für Palaeontologie und Geologie), Munich, Bavaria, Germany
FMUF	Florida Museum of Natural History, University of Florida, Gainesville, Florida, U.S.A.
GBIU	Department of Geological Sciences and Biology, Indiana University, Bloomington, Indiana, U.S.A.
GDVU	Geology Department of Victoria University, Wellington, Victoria, Australia
GPUG	Geological-Paleontological Institute, University of Göttingen (= Geologisch-Paläontologisches Institut, Universität Göttingen), Göttingen, Lower Saxony, Germany
HLDG	Museum Wiesbaden (= Hessischen Landesmuseums), Darmstadt, Hesse, Germany
IEUH	Institute of Evolution, University of Haifa, Israel
IGUSP	Institute of Geoscience, University of São Paulo (= Instituto de Geociências, Universidade de São Paulo), São Paulo, Brazil
MCNV	Museum of Natural Science in Valencia (= Museo de Ciencias Naturales de Valencia), Valencia, Spain
MPEF	Egidio Feruglio Paleontologic Museum (= Museo Paleontólogico Egidio Feruglio), Trelew, Chubut, Argentina
MVVA	National Museum of Victoria, Victoria, Australia
NMPC	National Museum (= Národní Muzeum or Musei Nationalis Pragae), Prague, Czech Republic
PIRAS	Paleontological Institute, Russian Academy of Sciences, Moscow, Russia
PMNH	Peabody Museum of Natural History, Yale University, New Haven, Connecticut, U.S.A.
QMSB	Queensland Museum, South Brisbane, Queensland, Australia
TBMM	Thomas Burke Memorial Museum, University of Washington, Seattle, Washington, U.S.A.
UCMP	University of California Museum of Paleontology, Berkeley and Davis, California, U.S.A.
USNM	United States National Museum of Natural History, Washington, DC, U.S.A.

Nomenclatural note. We use the original endings for species names that are combined with *Stigmellites*, despite the fact that generic names ending with the suffix "*-ites*" should be considered as masculine (International Commission on Zoological Nomenclature 1999, article 30.1.4.4). All adjectival species names published as *Stigmellites* have feminine endings, showing the intent of the authors. We follow the practice of lepidopterists to retain the original spelling. This practice is in accordance with a resolution adopted by the Societas Europaea Lepidopterologica in 2002 (Sommerer 2002).

Photography. Photographs of dried or fresh leaf mines were taken using a dark-field illumination setup on either a Zeiss Axioskop H or Zeiss Discovery.V20 microscope with a Zeiss AxioCam MR5 and AxioVision version SE64 4.9 software. Partial photographs were merged using the Adobe Photoshop CS6 photomerge tool and optimized by adjusting levels and curves. Photography of the fossil mines were done on a Canon EOS 500 camera with an EFS 60mm macro lens, accompanied by various combinations of low-angle indirect or direct illumination to accentuate subtle leaf-mine features. Processing of photo images were done by standard Photoshop methods, except for Fig. 10, which is an archival black-and-white photograph processed by standard darkroom techniques. Adobe Indesign CC was used to assemble individual images into a plate.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FIGURES 1–9. Leafmines of selected extant Nepticulidae from the Naturalis collection. **1.** *Acalyptris loranthella* (Klimesch) on *Loranthus europaeus* (Loranthaceae) near Foloi, Greece (EvN2011367). **2.** *Stigmella oxyacanthella* (Stainton) on *Crataegus monogyna* (Rosaceae) near Wassenaar, The Netherlands (EvN2007118, RMNH.INS.12638). **3.** *Ectoedemia caradjai* (Groschke) on *Quercus pubescens* (Fagaceae) near Exokhori, Greece (EvN2011380–1). **4.** Undescribed *Stigmella* on *Berberis nervosa* (Berberidaceae) in Gifford Pinchot National Forest, Washington state, USA (EvN2010027). **5.** Undescribed *Trifurcula (Glaucolepis)* on *Wisteria* (Fabaceae) near Aomori, Japan (CD13060). **6.** *Roscidotoga callicomae* Hoare on *Callicoma serratifolia* (Cunoniaceae) in Lamington National Park, Queensland, Australia (EvN2004078). **7.** *Bohemannia pulverosella* (Stainton) on *Malus sylvestris* (Rosaceae) in Barendrecht, The Netherlands (Koster nr 2582). **8.** *Ectoedemia* (*Fomoria*) *septembrella* (Stainton) on *Hypericum perforatum* (Hypericaceae) in Losser, The Netherlands (Koster nr 1789). **9.** *Stigmella plagicolella* (Stainton) on *Prunus spinosa* (Rosaceae) in Losser, The Netherlands (Koster nr 1984). Photographs by CD and EJvN (6).

FIGURES 10–20. Fossil representatives of Nepticulidae. **10.** Nepticulidae *incertae sedis* on *Cercidiphillym* in Wyoming, USA, from the early Maastrichtian Stage, Late Cretaceous [#27]. **11.** Nepticulidae *incertae sedis* on *Sapindopsis beckeriana* in Kansas, USA, from the late Albian Stage, Early Cretaceous [#14]. **12.** *Bohemannia butzmanni* Fischer holotype in Baltic Amber from Russia, from the Lutetian Stage, Middle Eocene (Fischer no. 5058) [#4]. **13.** Nepticulidae *incertae sedis* on *Platanus raynoldsii* in Montana, USA, from the Danian Stage, Early Paleocene. [#28]. **14.** *Stigmellites kzyldzharica* Kozlov paratype on *Platanus ambicula* in Kazakhstan, from the Turonian Stage, Late Cretaceous [#20]. **15.** Nepticulidae *incertae sedis* on *Pandemophyllum kvacekii* in Nebraska, USA, from the late Albian Stage, Early Cretaceous [#13]. **16.** Detail of the lower mine on 15. **17.** Nepticulidae *incertae sedis* on *Anisodromum upchurchii* in Kansas, USA, from the late Albian Stage, Early Cretaceous [#17] **18.** Nepticulidae *incertae sedis* on an undetermined leaf of Platanaceae in Kansas and Nebraska, USA, from the late Albian Stage, Early Cretaceous [#12]. **19.** Nepticulidae *incertae sedis* of DT91 on *Zizyphoides flabella* in Montana, USA, from the Danian Stage, Early Paleocene [#30]. **20.** Nepticulidae *incertae sedis* of DT41 and DT91 on *Cercidiphyllum genetrix* in Montana, USA, from the Danian Stage, Early Paleocene [#31]. Photographs by CCL, EJvN (12), M. Kozlov (14) and M. Donovan (19, 20).


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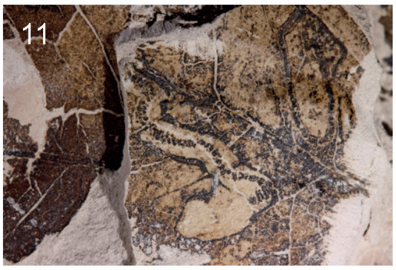
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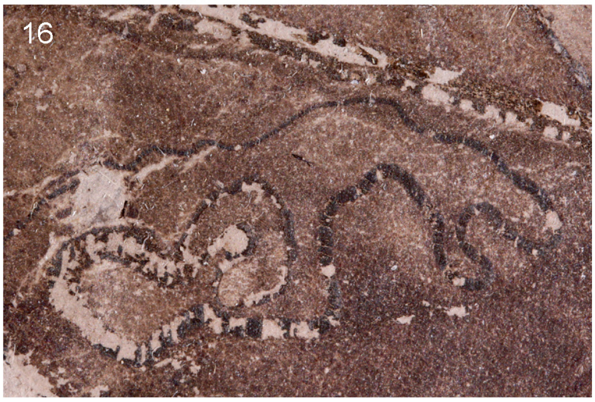
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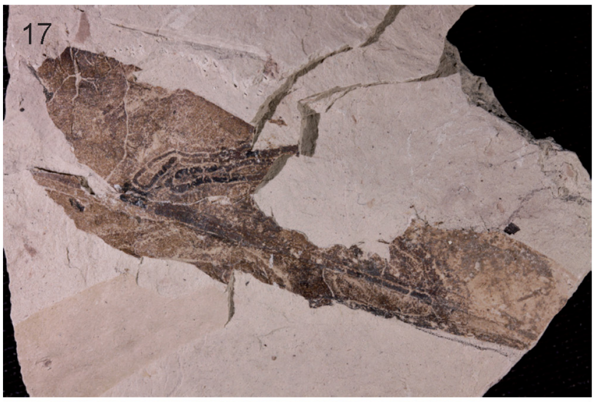
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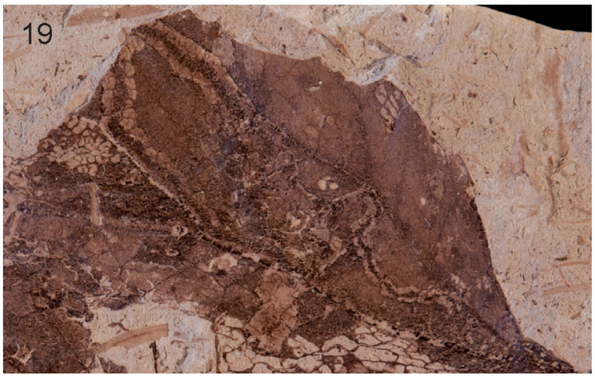
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Checklist

Adult body fossils

• # 1 *Ectoedemia* sp. [unverifiable]
Ectoedemia sp.; Skalski 1976: 199.
Ectoedemia sp.; Skalski 1990a: 127
Ectoedemia; Sohn *et al.* 2012: 22
• Adult in amber—[1 ex.] Coll: not stated
• Loc: Baltic Region (Baltic Amber)
• Stratum: Prussian Fm.; Lutetian Stage, middle Eocene
• Remarks: It is unclear as to what basis this fossil was assigned to *Ectoedemia*. There exists no description or images of the fossil. From his publications it is clear that Skalski used wing venation as one of the principal characters. If the venation had indeed been completely visible, assignment to *Ectoedemia* s. l. could be correct.

• # 2 *Stigmellites baltica* Kozlov, 1988
Stigmellites baltica Kozlov, 1988: 30, fig. 4
Stigmellites baltica; Skalski 1990a: 127
Stigmellites balticus; Sohn *et al.* 2012: 24
• Adult in amber—[1 ex.] Coll: Lost: stolen by thieves from the collection of K. M. Sadilenko, Moscow, Russia (HT: no. 15–1–4)
• Loc: Baltic Region (Baltic Amber)
• Stratum: Prussian Fm.; Lutetian Stage, middle Eocene
• Remarks: Unfortunately the holotype could not be studied, as the original material was lost during a robbery (Kozlov pers. comm.). The illustrated and described venation mostly resembles modern *Stigmella*, but other genera cannot be excluded.

• # 3 *Bohemannia aschaueri* Fischer, 2013
Bohemannia aschaueri Fischer, 2013: 88, fig. 3.
• Adult in amber—[1 ex.] Coll: BPGM (HT: SNSB-BSPG 2013 I 94), Fischer no. 5199
• Loc: Russia: Amber mine at Yantarny
• Stratum: Blaue Erde horizon, Prussian Fm.; Lutetian Stage, middle Eocene (Ritzkowski 1997)
• Remarks: The right wing shown in Fischer's Fig. 3d is a hindwing. The drawn short-side vein of vein number 3 (Cu) is, in our opinion, absent, which makes the hindwing venation identical to many modern Nepticulidae, including *Bohemannia*. The abdominal tip is wide, but the specimen is a male; male genitalia could be revealed during a preliminary micro CT scan. The forewing shows purplish scales, much as in modern *Bohemannia*. The venation, size, broad habitus and colour confirm the generic attribution: the species resembles modern *B. quadrimaculella* (Boheman), which is the type species of the genus. [Specimen examined by EJvN].

• # 4 *Bohemannia butzmanni* Fischer, 2013 (Fig. 12)
Bohemannia butzmanni Fischer, 2013: 86, fig. 1.
• Adult in amber—[1 ex.] Coll: BPGM (HT: SNSB-BSPG 2013 I 93) ex coll. Fischer no. 5058
• Loc: Russia: Amber mine at Yantarny
• Stratum: Blaue Erde horizon; Prussian Fm.; Lutetian Stage, middle Eocene (Ritzkowski 1997)
• Remarks: The venation of the holotype is identical to that of modern *Bohemannia*. The specimen has a broad, blunt abdomen, and most likely is a female. The extensions that are termed 'valvae' in the original description are probably protruding scales. The specimen is not significantly different from the holotype of *B. aschaueri* (#3), and they could well be conspecific. [Specimen examined by EJvN].

• # 5 cf. Stigmella sp.
Nepticulidae; Fischer 2013: 86, fig. 2
• Adult in amber—[1 ex.] Coll: Fischer collection no. 5217, possibly also 5058

- Loc: Russia: Amber mine at Yantarny
- Stratum: Blaue Erde horizon, Prussian Fm.; Lutetian Stage, middle Eocene (Ritzkowski 1997)
- Remarks: According to the author, this specimen may be conspecific with *Bohemannia butzmanni* (# 4). We disagree with that possibility: the forewing venation clearly differs, with fewer terminal branches of R+M (3 rather than 4 or 5); the antennae are much shorter (20 segments in a complete antenna versus incomplete antenna with at least 35 segments for *Bohemannia*); and the individual flagellomeres are longer, whereas those in *Bohemannia* (and many *Ectoedemia*) are short. This specimen most likely belongs to *Stigmella*. [Specimen examined by EJvN].

• # 6 Nepticulidae: incertae sedis

Nepticulidae; Fischer 2013: 88, fig. 4
- Adult in amber—[1 ex.] Coll: Fischer collection no. 5198
- Loc: Russia: Amber mine at Yantarny
- Stratum: Blaue Erde horizon, Prussian Fm.; Lutetian Stage, middle Eocene (Ritzkowski 1997)
- Remarks: Unfortunately the venation cannot be seen, and initial study with micro-CT scans has not yet provided a clear view of the specimen. This specimen could be a *Stigmella*, but an alternative genus also is possible. [Specimen examined by EJvN].

• # 7 Nepticulidae: incertae sedis

Nepticulidae; Fischer 2013: 91, fig. 5
- Adult in amber—[1 ex.] Coll: Fischer collection no. 5166
- Loc: Russia: Amber mine at Yantarny
- Stratum: Blaue Erde Horizon, Prussian Fm.; Lutetian Stage, middle Eocene (Ritzkowski 1997)
- Remarks: Re-examination of the fossil has not yet resulted in more precise identification. [Specimen examined by EJvN].

• # 8 cf. *Stigmella* sp.

Incurvariina or Nannolepidoptera species A; Jarzembowski 1980: 270, fig. 50
Stigmellites; Kozlov 1988: 32
Stigmellites; Sohn *et al.* 2012: 25
- Adult impression—[1 ex.] Coll: BMNH (I.9492)
- Loc: United Kingdom: England, Isle of Wight, Bembridge Marls
- Stratum: Bouldnor Fm.; late Priabonian Stage, late Eocene
- Remarks: This is one of two known adult impression fossils. Kozlov was the first to notice that the venation is clearly nepticulid. We think that the venation most closely resembles *Stigmella*, but there are insufficient visible veins to completely exclude *Acalyptris*.

• # 9 Nepticulidae: *incertae sedis*

Tineoidea species C; Jarzembowski 1980: 271, fig. 57
Stigmellites; Kozlov 1988: 32
Stigmellites "Species B"; Sohn *et al.* 2012: 26
- Adult impression—[1 ex.] Coll: BMNH (In.64540)
- Loc: United Kingdom: England, Isle of Wight, Bembridge Marls
- Stratum: Bouldnor Fm.; late Priabonian Stage, late Eocene
- Remarks: This is one of two known adult impression fossils. It is listed as "species B" in Sohn *et al.* (2012), but species B in Jarzembowski (1980) is not depicted and is referred perhaps to *Heliozela*. Kozlov (1988) places Jarzembowski's species A (see record # 8) and species C (this record) in *Stigmellites*. The venation is incomplete, but resembles a nepticulid. The hindwing shows a trifurculine condition of Rs+M, which is characteristic for the genus *Trifurcula*, but we find assignment to that genus premature.

• # 10 *Acalyptris* sp. [unverifiable]

Niepeltia sp.; Skalski 1990a: 127
Acalyptris; Skalski 1990b: 144

Acalyptris; Sohn *et al.* 2012
- Adult in copal—[1 ex.] Coll: not stated
- Loc: Tanzania: Zanzibar Island
- Stratum: East African Copal from unconsolidated sediments (Holocene Stage)
- Remarks: This fossil has been assigned to *Acalyptris*, although the characters to base this identification have not been indicated. Judging from Skalski's other publications he likely used wing venation as a leading character, which is quite characteristic for this genus (van Nieukerken 1986). There are no images or drawings of the fossil, nor is there the option to study the object due to an absence of reference to a collection. We leave this fossil in *Acalyptris* because there are no inconsistencies in characters and it involves an almost modern subfossil specimen.

• # 11 *Enteucha* sp. [unverifiable]
Johanssonia; Skalski 1976: 199
Johanssoniella; Sohn *et al.* 2012: 22
- Adult in copal—[1 ex.] Coll: not stated
- Loc: unclear
- Stratum: unclear, but undoubtedly copal from unconsolidated sediments of Pleistocene or Holocene Age.
- Remarks: The locality is unclear, although it was likely the Baltic region (Skalski 1976). In the publication, it was listed as *Johanssonia* Borkowski in a table with specimens from Baltic Amber: "avec un seule espèce fossile non encore décrite" [with a single undescribed fossil species]. A footnote however indicates that this fossil was embedded in copal instead of Baltic Amber and is thus essentially modern in age, compared to the other specimens in the table. There are no images or drawings, only the mention that it was placed in the genus *Johanssonia*. *Johanssoniella* Koçak, 1981 is a replacement name for *Johanssonia* Borkowski, 1972, but both are subjective junior synonyms of the extant genus *Enteucha* Meyrick, 1915 (synonymised by van Nieukerken 1986). There is no reference to a collection.

Leaf-mine fossils

• # 12 Nepticulidae: *incertae sedis* multiple species (Fig. 18)
Ectoedemia; Labandeira *et al.* 1994: 12279, figs. 1a–d
Ectoedemia; Sohn *et al.* 2012: 21
- Leaf mine—Host: Platanaceae: indeterminate genus—[11 exx.] Coll: FMUF (UF12701; UF7255 etc.)
- Loc: USA: Kansas and Nebraska, Braun Ranch, Hoisington and other localities
- Stratum: Dakota Fm.; late Albian Stage, Early Cretaceous
- Remarks: There are 11 leaf mines on Platanaceae, and one leaf mine on an undesignated host. Kristensen & Skalski (1998) cited this record as the earliest fossil evidence of Nepticulidae and also of the extant genus *Ectoedemia*. The original dating of these fossils was 97 Ma (Labandeira *et al.* 1994). However, by a combination of recent stratigraphic evaluation of the Dakota Formation (Brenner *et al.* 2000), and updates in global geochronological tie-points (Ogg *et al.* 2008), the lower portion of the Dakota Formation is re-dated at 102 Ma. We consider it impossible that these mines are related to modern *Platanus* feeders in the genus *Ectoedemia*, which belong to a much later evolved, subordinate clade (Doorenweerd *et al.* 2015), even though there is a superficial resemblance.

• # 13 Nepticulidae: *incertae sedis* (Figs 15, 16)
Stigmella; Labandeira *et al.* 1994: 12279, 12280, fig. 1e
cf. Stigmella; Sohn *et al.* 2012: 23
- Leaf mine—Host: Laurales: *Pandemophyllum kvacekii* Upchurch and Dilcher, 1990—[1 ex.] Coll: FMUF (UF12712)
- Loc: USA: Nebraska, Rose Creek
- Stratum: Dakota Fm.; late Albian Stage, Early Cretaceous
- Remarks: The mines resemble modern *Stigmella*, but because these cannot be separated from several other genera, we consider them as Nepticulidae *incertae sedis*. Sohn *et al.* (2012) combined this record with the

following two, but due to their occurrence on different host plants, we separate them here. There are no records of extant Nepticulidae feeding on Laurales.

• # 14 Nepticulidae: *incertae sedis* (Fig. 11)
Stigmella; Labandeira *et al.* 1994: 12279, 12280, figs. 1f–g
cf. Stigmella; Sohn *et al.* 2012: 23
• Leaf mine—Host: Platanaceae: *Sapindopsis beckeriana* Wang, 2002—[1 ex.] Coll: FMUF (UF4811)
• Loc: USA: Kansas, Hoisington
• Stratum: Dakota Fm.; late Albian Stage, Early Cretaceous
• Remarks: See record # 13 for remarks, only differing in host plant. *Sapindopsis* is one of the earliest appearing lineages of Platanaceae, confined to the Cretaceous and consists of pinnately-compound leaves. The specimen illustrated in Fig. 11 is a leaf-mined leaflet.

• # 15 Nepticulidae: *incertae sedis*
Stigmella; Labandeira *et al.* 1994: 12279, 12280, fig. 1h
cf. Stigmella; Sohn *et al.* 2012: 23
• Leaf mine—Host: Sapindales (family uncertain): *Anisodromum wolfei* Upchurch and Dilcer, 1990—[1 ex.] Coll: FMUF (UF12718)
• Loc: USA: Nebraska, Rose Creek—Dakota Fm.
• Stratum: late Albian Stage, Early Cretaceous
• Remarks: see record # 13 for remarks, only differing in host plant. Originally the higher host ranking was indicated as "Rosidae", however, based on the taxonomic framework of Bell *et al.* (2010) and classification of Wang (2002), this plant would be in the (Order) Sapindales.

• # 16 cf. Nepticulidae
Stigmella; Labandeira 1998: 110, fig. 3d
cf. Stigmella; Sohn *et al.* 2012: 22
• Leaf mine—Host: Laurales: *?Pabiania*—[1 ex.] Coll: FMUF (UF7252)
• Loc: USA: Kansas, Cloud Co., Braun's Ranch
• Stratum: Dakota Fm.; late Albian Stage, Early Cretaceous
• Remarks: Kristensen and Skalski (1998) cited this record in addition to the following as the earliest fossil evidence of Nepticulidae and also of the extant genus *Stigmella*. The mine is very long for a nepticulid mine and not clearly increasing in width; it perhaps resembles more an epidermal type of mine like those created by species of *Phyllocnistis* (Gracillariidae). There are no records of extant Nepticulidae feeding on Laurales.

• # 17 Nepticulidae: *incertae sedis* (Fig. 17)
Stigmella; Labandeira 1998: 110, fig. 3e
cf. Stigmella; Sohn *et al.* 2012: 22
• Leaf mine—Host: Sapindales (family uncertain): *Anisodromum upchurchii* Wang, 2002—[1 ex.] Coll: FMUF (UF16173)
• Loc: USA: Kansas, Cloud Co., Braun's Ranch
• Stratum: Dakota Fm.; late Albian Stage, Early Cretaceous
• Remarks: Kristensen and Skalski (Kristensen & Skalski 1998) cited this record as well as the former occurrence as the earliest fossil evidence of Nepticulidae and the extant genus *Stigmella*. The mine appears very nepticulid-like, but can belong to a number of different genera.

• # 18 Nepticulidae: *incertae sedis* multiple species
Nepticulidae Mine type KLmla, KLm1b, KLm1c, KLm2, KLm3, KLm11; Stephenson 1991: 154–156, 163
cf. Stigmella/Nepticulidae; Sohn *et al.* 2012: 23, 26
• Leaf mine—Host: Angiosperms—[32 exx.] Coll: GBIU (IU15706–4811; IU15706–7525; IU15706–7528; IU15709–4818; IU15709–7531; IU15709–7535; IU15706–4539; IU15706–7521; IU15706–7525; IU15706–7527; IU15706–4810; IU15703–3856; IU15703–7523a; IU15706–7255; IU15706–7256; IU15709–3950; IU15709–

4819; IU15713–4696; IU15713–4834; IU15713–4936; IU15713–7242; IU15713–7243; IU15713–7244; IU15713–7245; IU15713–7246; IU15723–7247; IU15713–7248; IU15713–7249; IU15713–7324; IU15706–4536; IU15706–7113; IU15714–7250)

• Loc: USA: Kansas and Nebraska, Braun Ranch, Hoisington and other localities (Dakota Fm.)

• Stratum: late Albian Stage, Late Cretaceous

• Remarks: The author compared these fossil mines with dried leaf mines from the Hering collection (BMNH), and suggests recent analogues for different types of leaf mines. Records 12 and 18 were combined by Sohn *et al.* (2012) but actually represent specimens from different time intervals. Record # 18 was also mentioned separately by Sohn *et al.* (2012: 26).

• # 19 *Stigmellites serpentina* Kozlov, 1988

Nepticulidae; Skalski 1979: 64
Stigmellites serpentina Kozlov, 1988: 32, pl. 2: 2
Stigmellites serpentina; Skalski 1990a: 127
Nepticulidae; Boucot 1990: 108, fig. 102
Stigmellites serpentina; Sohn *et al.* 2012: 25, 26

• Leaf mine—Host: Cercidiphyllaceae: *Trochodendroides arctica* Heer—[3 exx.] Coll: PIRAS (HT: PIN 2383/205)

• Loc: Kazakhstan: Kyzyl Orda Prov., Chilinsky, northwest spur of Karatau Mountain range, Kyzyl-Dzhar

• Stratum: Beleuty Fm.; Turonian Stage, Late Cretaceous

• Remarks: This occurrence was split into two records by Sohn *et al.* (2012), one referring to Skalski and Boucot on page 26 and one to Kozlov on page 25. However, the photograph published in Boucot (1990), referring to Skalski (1979), shows the entire leaf with three mines, of which Kozlov depicted a single mine and used it to designate the holotype. The image published by Kozlov is a mirror, facsimile version of the original. This mine was listed by Sohn *et al.* (2012) as occurring during the Oxfordian–Kimmeridgian Stages of the Late Jurassic, which would make this record represent by far the oldest nepticulid fossil. Nevertheless, Kozlov (1988) and Boucot (1990) cited the Turonian Stage of the early Late Cretaceous as the age for this occurrence. At Karatau, in the mountains of southernmost Kazakhstan, there are two intervals of strata bearing insects and plants, occurring in vertical succession. The older deposits are, indeed, Late Jurassic, and belong to the Oxfordian and Kimmeridgian Stages. The younger deposit is of early Late Cretaceous Age (Turonian Stage), and also contains fossil plants and insects of similar age. It appears that these two sequences were confused and geochronologically reversed (Friis *et al.* 2011); we consider the Turonian Stage the correct date for this record. Skalski (1979) cited this as a leaf mine from Karatau, "very similar to leaf mines produced by some existing species, e.g. *Nepticula tityrella* Stainton". We agree that this mine very much resembles modern Nepticulidae and is attributable to several constituent genera.

• # 20 *Stigmellites kzyldzharica* Kozlov, 1988 (Fig. 14)

Eriocraniidae; Zherikhin 1978: 79
Nepticulidae; Skalski 1979: 64
Nepticulidae; Zherikhin 1980: 89
Stigmellites kzyldzharica Kozlov, 1988: 32, fig. 5, pl. 2: 1
Stigmellites kzyldzharica; Skalski 1990a: 127
eriocranid; Grimaldi & Engel 2005: 572, fig. 13: 32.
Stigmellites kzyldzharicus; Sohn *et al.* 2012: 25

• Leaf mine—Host: Platanaceae*: Platanus ambicula* Vachr.– [2 exx.] Coll: PIRAS (HT: PIN 2383/206; PT: PIN 2383/214)

• Loc: Kazakhstan: Kyzyl Orda Prov., Chilinsky, northwest spur of Karatau Mountain Range, Kyzyl-Dzhar

• Stratum: Beleuty Fm.; Turonian Stage, Late Cretaceous

• Remarks: The mine is very long and narrow, and resembles somewhat modern *Acalyptris* mines. Extant *Platanus* species are host for *Acalyptris platani* (Müller-Rutz) in Europe (van Nieukerken 2007) and for three *Ectoedemia* species in North America (Wilkinson & Newton 1981; Doorenweerd *et al.* 2015).

• # 21 *Stigmellites samsonovi* Kozlov, 1988

Stigmellites samsonovi Kozlov, 1988: 33, pl. 2: 3

Stigmellites samsonovi; Skalski 1990a: 127
Stigmellites samsonovi; Zherikhin 2002: 321, fig. 475
Stigmellites samsonovi; Sohn *et al.* 2012: 25
- Leaf mine—Host: Cercidiphyllaceae: *Trochodendroides arctica* Heer—[1 ex.] Coll: PIRAS (HT: PIN 2383/209)
- Loc: Kazakhstan: Kyzyl Orda Prov., Chilinsky, northwest spur of Karatau Mountain Range, Kyzyl-Dzhar
- Stratum: Beleuty Fm.; Turonian Stage, Late Cretaceous
- Remarks: The mine begins as a narrow gallery and abruptly expands into a blotch, as seen with many extant *Ectoedemia* (s. str.) species, but also some leaf-mining species in other genera. This specimen is likely to be a nepticulid mine.

• # 22 *Stigmellites sharovi* Kozlov, 1988
Stigmellites sharovi Kozlov, 1988: 33, pl. 2: 4
Stigmellites sharovi; Skalski 1990a: 127
Stigmellites sharovi; Sohn *et al.* 2012: 25
- Leaf mine—Host: Cercidiphyllaceae: *Trochodendroides arctica* Heer—[1 ex.] Coll: PIRAS (HT: PIN 2383/208)
- Loc: Kazakhstan: Kyzyl Orda Prov., Chilinsky, northwest spur of Karatau Mountain Range, Kyzyl-Dzhar
- Stratum: Beleuty Fm.; Turonian Stage, Late Cretaceous
- Remarks: The attribution of this mine to the Nepticulidae seems likely.

• # 23 *Stigmellites tyshchenkoi* Kozlov, 1988
Stigmellites tyshchenkoi Kozlov, 1988: 33, pl. 2: 5
Stigmellites tyshchenkoi; Skalski 1990a: 127
Stigmellites tyshchenkoi; Zherikhin 2002: 321, fig. 475
Stigmellites tyshchenkoi; Sohn *et al.* 2012: 25
- Leaf mine—Host: Platanaceae: *Platanus latior* (Lesquereux) Knowlton—[1 ex.] Coll: PIRAS (HT: PIN 2383/211)
- Loc: Kazakhstan: Kyzyl Orda Prov., Chilinsky, northwest spur of Karatau Mountain Range, Kyzyl-Dzhar
- Stratum: Beleuty Fm.; Turonian Stage, Late Cretaceous
- Remarks: The photographs in both publications show rather different views of the same mine. The photograph of the mine in Kozlov (1988) appears to be free of frass, a feature which is also stated in the description ("no excrement line visible"). By contrast, in Zherikhin (2002) there is a clear black frass line with a fine margin from the edges of the mine. The original photographs from Kozlov (1988), now are available on http://nepticuloidea.info/nepticuloidea/stigmellites-tyshchenkoi, reveals that the frass likely is a very shiny and black. This image was overexposed during photography, making the specimen seem devoid of frass. We believe the fossil and photographs actually contain two mines. See also #20, which differs by one mine having a thin frass line.

• # 24 *Stigmellites resupinata* (Krassilov, 2008) comb. nov.
Lepidoptera; Krassilov 2007: 14, fig 1D,E
Ophiheliconoma resupinata Krassilov, 2008b: 100, pl. 34: 1,2
- Leaf mine—Host: Family unknown: *Dewalquea gerofitica* (Dobruskina) Krassilov—[1 ex.] Coll: IEUH, (HT IG1–139)
- Loc: Israel: southern Negev, Gerofit
- Stratum: mid-Turonian Stage, Late Cretaceous
- Remarks: Krassilov used an ichnotaxonomic ranking that cannot easily be correlated with extant taxonomic ranks. In the species description it is mentioned that the mine is "nepticuliform," and the number of instars (likely 6) appear to match that of extant *Stigmella*. However, most *Stigmella* have 4 or 5 instars. In Krassilov (2007), the detailed image (fig. 1E) is mentioned to depict an "end-blotch … with a hibernating cocoon." However, in Krassilov (2008), this section was re-interpreted as an intestiniform beginning of the mine, gradually increasing in width, which we also believe as more likely. The ovoidal scar mentioned at the oviposition site might equally be an egg-capsule. The original species description did not assign the species to a higher rank, rendering it a *nomen nudum*. However, we believe that the combined evidence is sufficient to assign this mine to Nepticulidae. The higher taxonomic rank for the host is possibly Myrtales or Rhizophorales (now placed in Malpighiales) (Krassilov 2008b), and the host species was an early angiosperm that had a mangrove-like habit.

• # 25 Nepticulidae: *incertae sedis* [unverifiable]
cf. Stigmella; Donner & Wilkinson 1989: 9
cf. Stigmella; Sohn *et al.* 2012: 22
• Leaf mine—Coll: Christopher Wilkinson
• Loc: Kazakhstan
• Stratum: Beleuty Fm.; Turonian Stage, Late Cretaceous
• Remarks: Wilkinson had borrowed several specimens that he reports as "exactly similar to *Stigmella* today", from a deposit he claims to be 110 Ma, but also states that it is the same age as Turonian (= 89.8—93.3 Ma). No further details are given. It is possible that this literature record refers to the more recent, Late Cretaceous, fossils from Kazakhstan, as in records # 19–23.

• # 26 Nepticulidae: *incertae sedis*
Stigmella; Labandeira *et al.* 2002: 2062, fig. 1h
cf. Stigmella; Sohn *et al.* 2012: 23
• Leaf mine—Host: Rosaceae: aff. *Rubus*—[1 ex.] Coll: YPM (6367a)
• Loc: USA: SW North Dakota, Williston Basin, near Marmarth
• Stratum: Hell Creek Fm.; latest Maastrichtian Stage, Late Cretaceous
• Remarks: In Labandeira *et al.* (2002) the host was identified as "Rosaceae"; in Sohn *et al.* (2012), it was listed as "*cf. Rubus*". The leaf with the mine exactly matches leaf morphotype HC80, designated as "aff *Rubus*" in Johnson (2002), from the Hell Creek flora of the Williston Basin. The leaf is morphologically consistent with modern-day *Rubus*, but a Late Cretaceous age seems unlikely for this modern genus.

• # 27 Nepticulidae: *incertae sedis* DT43 (Fig. 10)
Nepticulidae/*Stigmella*; Labandeira 2002a: 49, 252, fig. 2.10e–f
Nepticulidae; Sohn *et al.* 2012: 26
• Leaf mine—Host: Cercidiphyllaceae: *Cercidiphyllum* sp.—[1 ex.] Coll: USNM
• Loc: USA: Wyoming, Washakie Co., Big Cedar Ridge
• Stratum: Meeteetsee Fm.; early Maastrichtian Stage, Late Cretaceous
• Remarks: Only part of the mine is visible in the figure, but the specimen has the characteristics of a Nepticulidae mine. In the figure caption the mine is mentioned to be nepticulid, but in the appendix of Labandeira (2002a), together with the supporting information for the specimens that are depicted, the leaf mine is identified as *Stigmella*.

• # 28 Nepticulidae: *incertae sedis Platanus* DT91, DT282 (Fig. 13)
Lepidoptera; Donovan *et al.* 2014: fig. 2a–h, fig. 3e
• Leaf mine—Host: Platanaceae: *Platanus raynoldsii* Newberry—[21 exx.] Coll: USNM (including USNM 560118; USNM 560119; USNM 560120; USNM 560113; USNM 498156; YPM 65939A)
• Loc: USA: Mexican Hat, eastern Montana, Custer Co.
• Stratum: Fort Union Fm.; Danian Stage, early Paleocene
• Remarks: The authors identified material by damage type for each insect order. 1073 leaves with varied insect damage were investigated. The figures in the publication show Lepidoptera leaf mines as DT91 and a likely Lepidoptera leaf mine as DT282; both are on *Platanus raynoldsii*. We believe these leaf mines are likely to be nepticulid.

• # 29 Nepticulidae: *incertae sedis Juglandiphyllites* DT91, DT105
Insect-feeding damage; Donovan *et al.* 2014: fig. 3j, fig. 5
• Leaf mine—Host: Family unknown: *Juglandiphyllites glabra* Manchester & Dilcher—[5 exx.] Coll: USNM (including USNM 560118; USNM 560119; USNM 560120; USNM 560113; USNM 498156; YPM 65939A)
• Loc: USA: Mexican Hat, eastern Montana, Custer Co.
• Stratum: Fort Union Fm.; Danian Stage, early Paleocene
• Remarks: The frass trail of DT91 mines on *J. glabra* differs from DT91 mines on other hosts from the same publication (# 28–# 35); the frass is spheroidal and spread out in a loose trail or is completely absent in some areas.

The distance between frass and pellet accumulations is greater than for similar mines occurring on other host plants. It is likely there are different species involved in these DT91 mines.

• # 30 Nepticulidae: *incertae sedis Zizyphoides* DT91 (Fig. 19)
Leaf mines; Donovan *et al.* 2014: fig. 8
• Leaf mine—Host: Trochodendraceae: *Zizyphoides flabella* (Newberry) Crane, Manchester & Dilcher—[6 exx.] Coll: USNM (including USNM 560118; USNM 560119; USNM 560120; USNM 560113; USNM 498156; YPM 65939A)
• Loc: USA: Mexican Hat, eastern Montana, Custer Co.
• Stratum: Fort Union Fm.; Danian Stage, early Paleocene
• Remarks: DT91 mines on *Z. flabella* originate near a secondary vein and loop around to the adjacent secondary vein, following it until termination. These mines are likely to be Nepticulidae. The host *Zizyphoides* is only known from fossil leaves, but is always found in conjunction with *Nordenskioldia*, which is only known from infructescences. *Zizyphoides* (leaves) and *Nordenskioldia* (fruits) are presumed to be congeneric and placed within Trochondendraceae (Pigg *et a*l. 2001).

• # 31 Nepticulidae: *incertae sedis Cercidiphyllum* DT41, DT91 (Fig. 20)
Leaf mines; Donovan *et al.* 2014: fig. 10e–g
• Leaf mine—Host: Cercidiphyllaceae: *Cercidiphyllum genetrix* (Newberry) Hickey—[2 exx.] Coll: USNM (including USNM 560118; USNM 560119; USNM 560120; USNM 560113; USNM 498156; YPM 65939A)
• Loc: USA: Mexican Hat, eastern Montana, Custer Co.
• Stratum: Fort Union Fm.; Danian Stage, early Paleocene
• Remarks: DT41 mines (Fig. 10e–k in Donovan *et al.*, 2014) mentioned in this publication are found on *Cercidiphyllum* over a period of 6 m.yr. (million years), but likely represent different species based on the different mine morphologies. Mines from the same host, also from Wyoming, have also been recorded from the latest Cretaceous (66–72.1 Ma), as record # 27. This indicates that the association between this host and Nepticulidae minimally spans approximately 13 m.yr.

• # 32 Nepticulidae: *incertae sedis* "*Populus*" DT91
Insect damage; Donovan *et al.* 2014: fig. 13e–f
• Leaf mine—Host: Cercidiphyllaceae?: "*Populus*" *nebrascensis* Newberry– [1 ex.] Coll: USNM (including USNM 560118; USNM 560119; USNM 560120; USNM 560113; USNM 498156; YPM 65939A)
• Loc: USA: Mexican Hat, eastern Montana, Custer Co.
• Stratum: Fort Union Fm.; Danian Stage, early Paleocene
• Remarks: The Late Cretaceous host is not *Populus* (hence its placement in quotes) and likely belongs to a family far removed from the Salicaceae. The host probably is or probably closely related to *Cercidiphyllum* (Cercidiphyllaceae). We believe this leaf-mine record likely to be nepticulid.

• # 33 Nepticulidae: *incertae sedis Browniea* DT91
Insect damage; Donovan *et al.* 2014: fig. 14e
• Leaf mine—Host: Cornaceae: *Browniea serrata* (Newberry) Manchester & Hickey—[1 ex.] Coll: USNM (including USNM 560118; USNM 560119; USNM 560120; USNM 560113; USNM 498156; YPM 65939A)
• Loc: USA: Mexican Hat, eastern Montana, Custer Co.
• Stratum: Fort Union Fm.; Danian Stage, early Paleocene
• Remarks: The host family Cornaceae (including Nyssaceae, to which *Browniea* was originally assigned) is used as a host by some *Ectoedemia* in North-America (Doorenweerd *et al.* 2015) and undescribed *Acalyptris* species in Asia (data EJvN). However, the mines of this record are different from the mines of extant Cornaceae-feeding species. Nonetheless, these mines likely belong to Nepticulidae.

• # 34 Nepticulidae: *incertae sedis* Dicot morphotype 1 DT36, DT91
Insect damage; Donovan *et al.* 2014: fig. 15a–c
• Leaf mine—Host: Dicot leaf morphotype 1—[2 exx.] Coll: USNM (including USNM 560118; USNM 560119;

USNM 560120; USNM 560113; USNM 498156; YPM 65939A)
- Loc: USA: Mexican Hat, eastern Montana, Custer Co.
- Stratum: Fort Union Fm.; Danian Stage, early Paleocene
- Remarks: A blotch mine (DT36) and gallery mine (DT91) likely represent two different species. The detailed image of the DT91 mine in figure 15 shows what seems to be an exquisitely preserved egg-capsule. We believe it likely is Nepticulidae.

• # 35 Nepticulidae: *incertae sedis Cercidiphyllum* DT41

Leaf mines; Donovan *et al.* 2014: fig. 10h–k
- Leaf mine—Host: Cercidiphyllaceae: *Cercidiphyllum genetrix* (Newberry) Hickey—[1 ex.] Coll: USNM (USNM 560151, USNM 560152, USNM 560153, USNM 560154)
- Loc: USA: Wyoming, Haz-Mat and Skeleton Coast sites
- Stratum: Fort Union Fm.; Danian Stage, late Paleocene
- Remarks: DT41, see comments under record # 31.

• # 36 *Stigmellites gossi* Jarzembowski, 1989

Mine type 1; Crane & Jarzembowski 1980: 632, figs. 6, 8
Stigmellites gossi Jarzembowski, 1989: 448
Stigmella sp.; Skalski 1990a
Stigmellites gossi; Sohn *et al.* 2012: 24
- Leaf mine—Host: Dicot—[2 exx.] Coll: BMNH (HT: In.64547; PT: In.64548)
- Loc: United Kingdom: Southern England, Berkshire, Newbury, Cold Ash
- Stratum: Reading Fm.; Thanetian Stage, late Paleocene
- Remarks: Crane and Jarzembowski (1980) stated that this mine is similar to an unidentified species of *Stigmella* on *Quercus cerris* L.. The fossil mine was compared with North American *Stigmella pomivorella* (Packard) and *Bucculatrix pomifoliella* (Clemens). We think that the assignment to Nepticulidae is probably correct.

• # 37 *Stigmellites centennis* Jarzembowski, 1989

Mine type 2; Crane & Jarzembowski 1980: 633, fig. 4, 9.
Stigmellites centennis Jarzembowski, 1989: 448
Stigmella sp.; Skalski 1990a
Stigmellites centennis; Sohn *et al.* 2012: 24
- Leaf mine—Host: ?Fabaceae—[1 ex.] Coll: BMNH (HT: In.64549)
- Loc: United Kingdom: S England, Berkshire, Newbury, Cold Ash
- Stratum: Reading Fm.; Thanetian Stage, late Paleocene
- Remarks: We do not find the illustrations sufficiently convincing that we can corroborate Jarzembowksi's suggestion that this specimen resembles modern *Stigmella hemargyrella* (Kollar). However, assignment to Nepticulidae certainly is possible.

• # 38 cf. Nepticulidae: *incertae sedis* multiple exemplars

"Healed wounds on leaf"; Brooks 1955: 4, 6, pl. 1: 5.
Nepticulidae; Opler 1973: 1321
Nepticulidae; Kozlov 1988: 30
Nepticulidae; Sohn *et al.* 2012: 26
- Leaf mine—Host: unknown angiosperm family: *Proteoides wilcoxensis* Berry—[multiple exx.] Coll: USNM
- Loc: USA: Tennessee, Henry Co., SW of Puryear
- Stratum: Claiborne Fm., Wilcox deposits; late Ypresian Stage, early Eocene
- Remarks: The combination of the references by Berry (1916) and Brooks (1955), as provided by Sohn *et al.* (2012), is incorrect. Brooks (1955) referred to Berry's (1916) plates as material that was different from the galleries that he described, and which he did not regard as leaf mines. According to Opler (1973), the specimen does represent a nepticulid, of which we are not completely convinced, but tentatively accept. In addition, the plant host *Proteoides* does not belong to the Proteaceae; its family assignment is unknown (Dilcher 1973).

• # 39 Nepticulidae: *incertae sedis* multiple species [unverifiable]
cf. Stigmella; Wilf *et al.* 2005: 8944
cf. Stigmella; Sohn *et al.* 2012: 24
• Leaf mine—Host: unidentified dicot—[multiple exx.] Coll: MPEF
• Loc: Argentina: Patagonia, Chubut, Laguna del Hunco
• Stratum: Tufolitas Laguna del Hunco Fm.; Ypresian Stage, early Eocene (Genise & Petrulevicius 2001).
• Remarks: The study counted 3599 instances of fossil leaf feeding; however, it was unspecified as to how many of these were nepticulid in affinity.

• # 40 Nepticulidae: *incertae sedis* DT37
leaf mines; Wilf *et al.* 2001: 6222, suppl. fig. 5b
mining DT37; Labandeira *et al.* 2007
• Leaf mine—Host: Fabaceae: "*Caesalpinia*"—[1 ex.] Coll: USNM (USNM 9623)
• Loc: USA: Utah, Uinta Basin
• Stratum: Green River Fm.; Lutetian Stage, middle Eocene
• Remarks: A photographic image of a fossil leaf mine of the type DT37, was provided as an example of a leaf mine. The same image is included is included in # 71. We find it likely that this specimen is a member of the Nepticulidae.

• # 41 Nepticulidae: *incertae sedis*
Stigmella; Labandeira 2002b: 45, figs. 4a–b
cf. Stigmella; Sohn *et al.* 2012: 22
• Leaf mine—Host: dicotyledonous angiosperm—[1 ex.] Coll: TBMM (57293a)
• Loc: USA: Washington, Whatcom Co., near Bellingham
• Stratum: Chuckanut Fm.; Lutetian Stage, middle Eocene
• Remarks: Judging from the image, the mine has the general impression of a nepticulid mine.

• # 42 Nepticulidae: *incertae sedis*
Stigmella; Labandeira 2002b: 45, figs. 4e–g
cf. Stigmella; Sohn *et al.* 2012: 22
• Leaf mine—Host: Rosaceae: *cf. Sorbus*—[1 ex.] Coll: TBMM (76477)
• Loc: USA: Washington State, Ferry Co., Republic
• Stratum: Klondike Mountain Fm.; Lutetian Stage, middle Eocene
• Remarks: The author stated that the fossil mine is particularly similar to those made by the extant *Sorbus*-feeding *Stigmella nylandriella* (Tengström) and *S. magdalenae* (Klimesch), that construct a thin, threadlike, central frass trail. The fossil mine could have been made by other genera as well; however, we suggest that it likely was made by Nepticulidae. *Sorbus* is an important host for extant Nepticulidae, with species of *Stigmella* and *Ectoedemia* that feed on this genus throughout the Palearctic, but Nepticulidae currently have not been found on this host in the Nearctic. However, it should be considered that there were close biogeographical connections between the Nearctic and the western Palearctic (via the North Atlantic Land Bridge) and between the Nearctic and eastern Asia (via Beringia) during the Paleocene and Eocene. Consequently, it comes as no surprise that the Nearctic Paleogene shares plant hosts and their insect herbivores with the western Palearctic and eastern Asia (Labandeira 2002b).

• # 43 Nepticulidae: *incertae sedis*
cf. *Stigmella*; Kinzelbach 1970: 94, 96, fig. 1
Order uncertain; Kozlov 1988: 54
cf. Stigmella; Sohn *et al.* 2012: 22
• Leaf mine—Host: Moraceae—[1 ex.] Coll: HLDG (Me7408)
• Loc: Germany: Hessen, S Frankfurt, near Darmstadt, Messel oil shale-layers
• Stratum: Messel Fm.; early Lutetian Stage, middle Eocene
• Remarks: Kinzelbach (1970) suggested "… mine shape matches the extant genus *Stigmella* …". The fossil is a compression between layers of compacted coal, from a drawing of the leaf and mine that was made. The mine has

the general outline of a nepticulid mine. Several extant species of *Stigmella* feed on Moraceae, mostly on various *Ficus* species (Gustafsson 1985; Puplesis 1994; Vári 1963), but also include a species from Japan on *Morus* (Hirano 2010).

• # 44 Nepticulidae *incertae sedis* [unverifiable]
Stigmellites spp.; Jarzembowski 1995: 146
Stigmellites; Sohn *et al.* 2012: 25
• Leaf mine—Host: not mentioned—[multiple exx.] Coll: BMNH
• Loc: United Kingdom: Hampshire, East Dorset, Bournemouth
• Stratum: Branksome Sand Fm.; Lutetian Stage, middle Eocene (McElwaine, 1998)
• Remarks: Jarzembowski (1995) is a publication without illustrations, and represents a checklist of Paleogene insects from Dorset.

• # 45 Nepticulidae: *incertae sedis*
Nepticulidae; Stephenson & Scott 1992: 547, figs. 5: b, d, e, f, h, figs. 6: d, e
Nepticulidae; Lang *et al.* 1995: 159–162, 165–168, 170, figs. 3a, 3b, 3d, 3g, 3h, 4a–g, 4i–k, 4m, 4n, pl. 2: 2, 3, 7, 9, pl. 3: 1–3, 5, 6
?Nepticulidae; Labandeira 2002a: 49, 252, fig. 2.10i–j
Nepticulidae; Sohn *et al.* 2012: 23
• Leaf mine—Host: Angiosperms—[13 exx.] Coll: BMNH (V.45868; V.48524; V.48798; V.49808; V.49905; V.50089; V.50460; V.50622; V.50698; V.50731; V.50733; V.50904; V.50952)
• Loc: United Kingdom: Hampshire, East Dorset, Bournemouth
• Stratum: Branksome Sand Fm.; Lutetian Stage, middle Eocene (McElwaine, 1998).
• Remarks: The authors used analogies to recent leaf mines from the Hering collection (BMNH) to characterize the fossils. They do not identify any specimen beyond that of the family, but often mention similarities to extant species of *Stigmella* on a range of different host plants.

• # 46 cf. *Stigmellites messelensis* Straus, 1976
Worm or larva; Bornhardt 1975: 471
Stigmellites messelensis Straus 1976: 446
Stigmellites messelensis; Kozlov 1988: 32
Stigmellites messelensis; Skalski 1990a: 127
Stigmellites messelensis; Sohn *et al.* 2012: 25
• Leaf mine—Host: Dicot—[1 ex.] Coll: unspecified private
• Loc: Germany: Hessen, S Frankfurt, near Darmstadt, Messel oil-shale layers
• Stratum: Messel Fm.; early Lutetian Stage, middle Eocene
• Remarks: The figure of the mine is rather unclear. The mine could be nepticulid, but given its small size, a bucculatricid affiliation also is a possibility. As identification of this mine awaits further study, we tentatively leave the species assigned to *Stigmellites*.

• # 47 cf. Nepticulidae: *incertae sedis*
Nepticulidae Leaf Mine Form 1–2; Rozefelds 1988a: 2, figs. 2a–d
?Nepticulidae; Sohn *et al.* 2012: 26
• Leaf mine—Host: unknown dicot—[2 exx.] Coll: MVVA (NMVP183063, NMVP183064)
• Loc: Australia: Victoria, Alcoa Anglesea Coal Mine
• Stratum: Eastern View Fm.; Priabonian Stage, late Eocene
• Remarks: These mines resemble modern nepticulid mines, but the illustrations are inconclusive. The two different types of illustrated mines may represent two species.

• # 48 cf. *Roscidotoga* sp.
Nepticulidae Leaf Mine Form 3; Rozefelds 1988a: 2, figs. 2e–f
?Nepticulidae; Sohn *et al.* 2012: 26

- Leaf mine—Host: Elaeocarpaceae—[1 ex.] Coll: MVVA (NMVP183065)
- Loc: Australia: Victoria, Alcoa Anglesea Coal Mine
- Stratum: Eastern View Fm.; Priabonian Stage, late Eocene
- Remarks: The single mine resembles very much a modern nepticulid mine. The genus *Roscidotoga* (Fig. 6) is an extant genus endemic to Australian rainforests and is specialized on hosts of Oxalidales, of which two species feed on Elaeocarpaceae (van Nieukerken *et al.* 2011a). The mine morphology fits that of *Roscidotoga*, but also several other nepticulid genera, including *Stigmella*. With this in mind, we assign the fossil mine with some doubt to *Roscidotoga*.

• # 49 Nepticulidae: *incertae sedis*

Nepticulidae Leaf Mine Form 4–5; Rozefelds 1988a: 4, figs. 3a–c
Nepticulidae; Labandeira 2002a: 49, 252, fig. 2.10k–l
?Nepticulidae; Sohn *et al.* 2012: 26

- Leaf mine—Host: Lauraceae—[5 exx.] Coll: MVVA (NMVP183063, NMVP183064, NMVP183065)
- Loc: Australia: Victoria, Alcoa Anglesea Coal Mine
- Stratum: Eastern View Fm.; Priabonian Stage, late Eocene
- Remarks: Rozefelds (1988a) considers both mine types on the same leaf as possibly belonging to two species. Rather, we think that these mine types belong to the same species. The left mine possibly is less developed. We doubt the presence of the large blotch as shown in the reconstruction (fig. 3D). If the host identification is correct, this is another example of an extinct host association, as we do not know of a single, extant nepticulid feeding on Lauraceae.

• # 50 *Stigmellites fossilis* (Heyden, 1862)

Nepticula fossilis Heyden, 1862: 77, pl. 10: 2
unidentified, may be dipterous; Opler 1973: 1321
Stigmellites fossilis; Kozlov 1988: 31
Stigmellites fossilis; Sohn *et al.* 2012: 24

- Leaf mine—Host: Juglandaceae: *Juglans acuminata* A. Braun—[1 ex.] Coll: originally collection of the Senckenberg Nature-Study Society, Frankfurt [not found, probably lost]
- Loc: Germany: Hessen, Bad Salzhausen [the locality in Sohn *et al.* (2012) is incorrect]
- Stratum: [unknown formation]; Chattian Stage, late Oligocene
- Remarks: Although no extant European Nepticulidae feed on Juglandaceae, this family is an important host family for Nepticulidae in North America and Asia that includes several species of *Stigmella* and *Ectoedemia* as leaf miners. The previously known occurrences of these genera would be expected on this European host. The illustrated mine clearly resembles extant nepticulid mines. The suggestion that this mine might belong to Diptera, indicated by Opler (1973,) is implausible, as Juglandaceae seems to be completely absent from the host record for extant leafmining Diptera, and certainly for Agromyzidae (Spencer 1990),. The Agromyzidae is the only dipteran leaf-mining clade known from the fossil record (Winkler *et al.* 2010).

• # 51 *Stigmellites almeidae* (Martins-Neto, 1989) comb. nov.

Nepticula? *almeidae* Martins-Neto, 1989: 381, pl. 1c, Fig. 5a
cf. Stigmella almeidae; Sohn *et al.* 2012: 22

- Leaf mine—Host: Symplocaceae: *cf. Symplocos* sp. A—[1 ex.] Coll: IGUSP (HT: GP/1T-1644)
- Loc: Brazil: São Paulo, Tremembé, along the road that connects Rodovia Presidente Dutra with Campos do Jordão
- Stratum: Tremembé Fm.; Chattian–Aquitanian Stages, late Oligocene–early Miocene boundary interval
- Remarks: The species was described initially as *Nepticula*, a junior synonym of *Stigmella*. We cannot reliably assign this fossil to *Stigmella*. Instead, we place it in the form-genus *Stigmellites*. From the images provided, it is difficult to judge if the specimen actually represents a nepticulid mine, although it is plausible. In eastern Asia (Taiwan), leaf mines of *Acalyptris* have been found on a species of *Symplocos* (EJvN, unpublished data).

• # 52 Nepticulidae: *incertae sedis*
leaf mine; Peñalver 1997: 150, fig. 1
Nepticulidae; Peñalver & Delclòs 2004: 82, fig. 6: 2. pl. 2: 2
Nepticulidae; Sohn *et al.* 2012: 26
• Leaf mine—Host: Lauraceae: *Laurophyllum*—[1 ex.] Coll: MCNV (MPV RIB-242)
• Loc: Spain: Castellón Prov., near Ribesalbes, "La Rinconada" site
• Stratum: bituminous rhythmites; Aquitanian Stage, early Miocene
• Remarks: The presence of multiple, independent mines on the same leaf occurs frequently in Nepticulidae, such as many *Stigmella* species that are known to feed on certain (sub)tropical plants. (The other alleged mine depicted by these authors is on the host *Celtis* sp. In our opinion, this feature is not a mine, but rather physical damage, where the leaf has been broken along its veinlets.)

• # 53 Nepticulidae: *incertae sedis* DT41
cf. Stigmella; Knor *et al.* 2012: 104, fig 2j
• Leaf mine—Host: Schisandraceae: *?Schisandra*—[multiple exemplars] Coll: NMPC, Bílina Mine Enterprise collections and Senckenberg Naturhistorische Sammlungen Dresden
• Loc: Czech Republic, North Bohemia
• Stratum: Most Fm.; Burdigalian Stage, early Miocene
• Remarks: Knor *et al.* (2012) identified material using the Labandeira *et al.* (2007) guide (# 71), in which one fossil is depicted as a *Stigmella*-like mine. Over 50 fossils are reported as leaf mines at this site, but it is not clear which of those likely are nepticulid or on which hosts the mines occur. A leaf mine classified as DT41 is depicted, which looks plausible for assignment to Nepticulidae. The damage type 41 exemplar shown in Labandeira *et al.* (2007), however, seems less likely a nepticulid, because its long length and pattern of vein crossing is more suggestive of a lyonetiid. If the host record is correct, it is the most basal angiosperm host record for Nepticulidae (see Table 1)
.

• # 54 *Stigmella* sp.
Stigmella; Liebhold *et al.* 1982: 456, figs. 1–2
Nepticulidae or perhaps Diptera; Kozlov 1988: 30
cf. Stigmella; Sohn *et al.* 2012: 23
• Leaf mine—Host: Berberidaceae: *Mahonia reticulata* (MacGinitie) Brown—[1 ex.] Coll: UCMP (8437)
• Loc: USA: Trapper Creek, Southern Idaho
• Stratum: Trapper Creek Fm.; early Langhian Stage, middle Miocene
• Remarks: The authors note the resemblance of the fossil mine to herbarium mines of undescribed *Stigmella* species on "*Mahonia" pinnata* (now *Berberis aquifolium*), also recorded on *Berberis nervosa* and *B. repens* hosts. We illustrate the mine of the extant species here (Fig. 4). No other Nepticulidae are known to feed on Berberidaceae hosts. We think it very likely that the fossil species is closely related to the extant species or possibly is a direct ancestor. The extant species is related to *Stigmella quercipulchella* (Chambers).

• # 55 *Stigmella* sp. [unverifiable]
Nepticula; Opler 1973: 1321
Nepticulidae; Kozlov 1988: 30
cf. Stigmella; Sohn *et al.* 2012: 23
• Leaf mine—Host: Fagaceae: *Quercus hannibali* Dorf—[1 ex.] Coll: UCMP
• Loc: USA: Nevada, Churchill Co., Buffalo Canyon
• Stratum: Buffalo Canyon Fm.; Langhian Stage, middle Miocene
• Remarks: *Quercus hannibali* is the fossil equivalent or very closely related species to extant *Q. chrysolepis* of California. The mine is not depicted. See # 61.

• # 56 Nepticulidae: *incertae sedis*
cf Nepticulidae; Lewis 1969: 1210, fig. 1
Caloptilia; Opler 1973: 1322

eriocraniid; Opler 1974b: 74
Nepticulidae; Kozlov 1988: 30
Stigmella sp.; Skalski 1990a: 127
Nepticula; Lewis *et al.* 1990: 7, fig. 3c
- Leaf mine—Host: Possibly Fagaceae: oak leaf.—[1 ex.] Coll: not stated
- Loc: USA: eastern Washington
- Stratum: Latah Fm.; Aquitanian–Serravallian Stages; early–middle Miocene
- Remarks: Opler (1973) identified the specimen as a *Caloptilia* mine, but later Opler (1974)—probably erroneously—cites it as an eriocraniid mine. There is no collection data provided, but on the figure there is "B16" noted on the slab. In 1990, Lewis *et al.* regarded the mine as *Nepticula*—the junior synonym of *Stigmella*. It is notable that the fossil of a small, apparently oak leaf that seemingly has marginal feeding also has a leaf mine whose trajectory follows the inner margin of the external feeding damage. This leaf mine very likely represents a nepticulid, probably *Stigmella*, but identification as an early phase of a *Caloptilia* mine cannot be excluded.

• # 57 *Stigmella* sp.
Nepticula; Opler 1973: 1321, fig. 1a
Nepticulidae; Kozlov 1988: 30
cf. Stigmella; Sohn *et al.* 2012: 23
- Leaf mine—Host: Fagaceae: cf. *Quercus virginiana* Mill.—[multiple exx.] Coll: UCMP
- Loc: USA: California, San Luis Obispo Co., Temblor Range
- Stratum: Temblor Fm.; ?Serravallian Stage, middle Miocene
- Remarks: The author mentioned that the fossil leaf mines essentially are identical to those created on *Quercus* by extant Californian leaf miners. The putative host *Q. virginiana* is an extant species of the southeastern United States. Although the depicted mine certainly appears plausibly nepticulid, any comparison with extant species from the same region should be done with care. There is a large variety of leafminer species feeding on *Quercus* worldwide, but particularly in western North America where the host genus is exceptionally diverse. Several *Stigmella* species, of which only one of which is formally named, are known to feed on Californian oaks. Present-day *Ectoedemia* mines have not been observed (coll. Essig Museum, coll. D.L. Wagner). Therefore, we consider it very likely that the fossil nepticulid mines on *Quercus*, as cited by Opler (1973), indeed belong to *Stigmella*.

• # 58 Nepticulidae: *incertae sedis* [unverifiable]
?*Nepticula*; Opler 1973: 1321
Nepticulidae; Kozlov 1988: 30
cf. Stigmella; Sohn *et al.* 2012: 23
- Leaf mine—Host: Fagaceae*: Quercus pseudolyrata* Lesquereux—Coll: UCMP
- Loc: USA: Oregon, Columbia Plateau, Blue Mountains, Stinking Water
- Stratum: Mascall Fm.; Serravallian Stage, middle Miocene
- Remarks: Not illustrated; the identity and affiliation remains uncertain

• # 59 Nepticulidae: *incertae sedis* ?multiple species [unverifiable]
Nepticulidae; Donner & Wilkinson 1989: 9
Nepticulidae; Sohn *et al.* 2012: 26
- Leaf mine—Host: not mentioned—[multiple exx.] Coll: GDVU
- Loc: New Zealand
- Stratum: [unknown formation]; middle Miocene
- Remarks: The authors mentioned fossil mines occurring in New Zealand that are similar to extant *Stigmella*. However, it is unclear if the fossil leaf-mine material that was referred to still exists and where it is deposited.

• # 60 Nepticulidae: *incertae sedis* [unverifiable]
Nepticulidae; Donner & Wilkinson 1989: 9
Nepticulidae; Sohn *et al.* 2012: 26
- Leaf mine—[2 exx.] Coll: not stated

- Loc: North America
- Stratum: [unknown formation]; Serravallian Stage, middle Miocene
- Remarks: Mentioned in the same paragraph as records # 25 and # 59. No further details.

• # 61 *Stigmella* sp. [unverifiable]
Nepticula; Opler 1973: 1321
Nepticulidae; Kozlov 1988: 30
cf. Stigmella; Sohn *et al.* 2012: 23
- Leaf mine—Host: Fagaceae: *Quercus hannibali* Dorf—[1 ex.] Coll: UCMP
- Loc: USA: Nevada, Nye Co., Cedar Mountains, Upper Goldyke
- Stratum: Esmeralda Fm.; Serravallian Stage, middle Miocene
- Remarks: *Quercus hannibali* is the fossil equivalent of extant *Q. chrysolepis*. The leaf mine mentioned in this record has not been illustrated in any publication. There is an undescribed species of *Stigmella* on *Q. chrysolepis*. See # 55.

• # 62 *Stigmella* sp.
Nepticula cf. *variella*; Opler 1973: 1322
Nepticula cf. *variella*; Opler 1974a: 74, pl. 7
Nepticulidae; Kozlov 1988: 30
Stigmella cf. *variella*; Skalski 1990a: 127
cf. Stigmella; Sohn *et al.* 2012: 23
- Leaf mine—Host: Fagaceae: *Quercus wislizenoides* Axelrod—[1 ex.] Coll: UCMP
- Loc: USA: Nevada, Storey Co., Dead Camel Range
- Stratum: Chloropagus Fm.; Serravallian Stage, middle Miocene
- Remarks: The author stated that the leaf mine "is indistinguishable from mines made by living *Nepticula variella* Braun." (“*Nepticula*” is a junior synonym of *Stigmella*). *Stigmella variella* feeds on the evergreen oaks, *Quercus agrifolia* Née (coastal live oak) and *Q. wislizeni* A. DC. (interior live oak) in California; the latter is the extant equivalent of the fossil *Q. wislizenoides* (Opler 1973).

• # 63 *Stigmella* sp. [unverifiable]
Nepticula; Opler 1973: 1321
Nepticulidae; Kozlov 1988: 30
cf. Stigmella; Sohn *et al.* 2012: 23
- Leaf mine—Host: Fagaceae: *Lithocarpus* or *Quercus simulata* Knowlton—[2 exx.] Coll: UCMP
- Loc: USA: Idaho, Thorn Creek
- Stratum: Payette Fm.; Serravallian–Tortonian Stages, middle to late Miocene
- Remarks: Not illustrated. See # 57. The table in Opler (1973) lists both *Lithocarpus* and *Quercus simulata* in the same row for a single host record. We find it likely that the host of this leaf mine is one of the two, but the identity was impossible to determine with high reliability. Axelrod (1995) also indicates that *Q. simulata* and *Lithocarpus* are regularly confused, and suggests that a number of specimens identified as *Q. simulata* from the Miocene outside the Purple Mountain flora represent actually *Lithocarpus*, which may be tentatively recognized by “coarse secondaries and often with a coarsely serrate margin”.

• # 64 *Stigmella* sp.
Stigmella; Kuroko 1987: 119, fig. 1
Stigmella; Kuroko 1990: 1, fig. 1
Stigmella sp.; Skalski 1990a: 127
cf. Stigmella; Sohn *et al.* 2012: 22
- Leaf mine—Host: Betulaceae: cf. *Betula grossa* Siebold & Zucc.—[1 ex.] Coll: Collection of Tachu Koshimizu
- Loc: Japan: central Honshu, at the border between Nagano and Gumma Prefectures
- Stratum: Kabutoiwa Plant Bed; Tortonian–Messinian Stages, late Miocene
- Remarks: A trace of the egg case is recognized in this specimen as a dark, brownish, elliptical spot. The host,

Betula grossa, is a common extant tree, with a rich nepticulid fauna in Japan, including populations of this host in Nagano Prefecture where this fossil was found. On the basis of the extant fauna and the shape of the mine, we can associate this mine with the genus *Stigmella*, but not with an extant species.

• # 65 *Stigmella* sp. [unverifiable]
Nepticula; Opler 1973: 1321
Nepticulidae; Kozlov 1988: 30
cf. Stigmella; Sohn *et al.* 2012: 23
• Leaf mine—Host: Fagaceae: *Quercus hannibali* Dorf—[1 ex.] Coll: UCMP
• Loc: USA: Nevada, Lyon Co., near Yerington
• Stratum: Aldrich Station Fm.; Zanclean Stage, early Pliocene
• Remarks: *Quercus hannibali* is the fossil equivalent of *Q. chrysolepis*. The mine is not depicted by a photographic image or line drawing. See # 57.

• # 66 *Stigmellites zelkovae* Straus, 1977
Stigmellites zelkovae; Straus 1977: 61, fig. 14
Stigmellites zelkovae; Skalski 1990a: 127
Stigmellites zelkovae; Sohn *et al.* 2012: 25
• Leaf mine—Host: Ulmaceae: *Zelkova*—[1 ex.] Coll: GPUG (HT: 23973)
• Loc: Germany: Niedersachsen, Willershausen am Harz
• Stratum: "Willershausen Shale"; Piacenzian Stage, late Pliocene (Brauckmann *et al.* 2001).
• Remarks: Straus (1977) attributed this fossil to *Stigmellites* because of its similarity to extant nepticulid leaf mines. A drawing of the mine was included, but there were no photographic images. Judging from the drawing, it could be a partial nepticulid mine, or a bucculatricid mine. There are extant *Stigmella* species known from *Zelkova* in Asia, such as *S. zelkoviella* Kemperman & Wilkinson from Japan (Kemperman *et al.* 1985), and an undescribed species from the Caucasus Region (Skala 1941). There is also an extant Bucculatricidae species known to feed on *Zelkova*: *Bucculatrix serratella* Kobayashi *et al.*, in Japan (Kobayashi *et al.* 2010).

• # 67 *Stigmellites carpiniorientalis* Straus, 1977 [unverifiable]
Stigmellites carpini-orientalis Straus, 1977: 60, fig. 80, 62
Stigmellites carpini-orientalis; Skalski 1990a: 127
Stigmellites carpiniorientalis; Sohn *et al.* 2012: 24
Leaf mine—Host: Betulaceae: *Carpinus orientalis* Mill.—[2 exx.] Coll: GPUG (HT: 22763; PT: 22134)
• Loc: Germany: Niedersachsen, Willershausen am Harz
• Stratum: "Willershausen Shale"; Piacenzian Stage, late Pliocene (Brauckmann *et al.* 2001)
• Remarks: The host is an extant species. The images are of insufficient quality to re-evaluate the mines. We tentatively leave this occurrence as *Stigmellites*. Currently, *Stigmella microtheriella* (Stainton) and *S. johanssonella* A. & Z. Laštuvka are known to feed on *Carpinus orientalis*. However, eastern Palearctic extant species of *Ectoedemia* also feed on *Carpinus*. We cannot exclude that this genus occurred on the same host in Europe during the Pliocene.

• # 68 cf. *Stigmella ulmivora* Fologne, 1860
Stigmella ulmivora; Kernbach 1967: 106 fig. 5
Stigmella ulmivora; Straus 1977: 61, fig. 12
Stigmella ulmivora; Kozlov 1988: 30
Stigmella ulmivora; Skalski 1990a: 127
cf. Stigmella ulmivora; Brauckmann *et al.* 2001: 33
cf. Stigmella ulmivora; Sohn *et al.* 2012: 22
• Leaf mine—Host: not stated—[1 ex.] Coll: GPUG (596–4–9111)
• Loc: Germany: Niedersachsen, Willershausen am Harz
• Stratum: "Willershausen Shale"; Piacenzian Stage, late Pliocene (Brauckmann *et al.* 2001)
• Remarks: According to Kernbach, this mine was identified by Hering as *S. ulmivora*, but he did not mention the

affiliation of the host. Considering the identification of the mine as *S. ulmivora*, the host is likely to be Ulmaceae. The base of the illustrated leaf host has not been preserved, which would be required for identification of the host as ulmaceous. This leaf mine represents the only fossil assigned to an extant species, which we believe is plausible, especially considering the recent age of the fossil. However, the totality of evidence is meagre. Moreover, even extant mines on *Ulmus* cannot be identified with certainty as belonging to either *S. ulmivora* or *S. ulmiphaga* (Preissecker) in the region where both occur (e.g. Laštůvka & Laštůvka 1997). We tentatively attribute this specimen to *Stigmella ulmivora*.

• # 69 *Stigmellites heringi* Kernbach, 1967 [unverifiable]
Stigmellites heringi Kernbach, 1967: 104, fig. 3
Stigmellites heringi; Straus 1977
Stigmellites heringi; Kozlov 1988: 30
Stigmellites heringi: Skalski 1990a: 127
Lepidoptera Suborder uncertain; Carpenter 1992: 380
Family uncertain; Brauckmann *et al.* 2001: 33
Stigmellites heringi; Sohn *et al.* 2012: 24
• Leaf mine—Host: Berberidaceae: *Berberis*—[1 ex.] Coll: GPUG (HT: 596–2–11137)
• Loc: Germany: Niedersachsen, Willershausen am Harz
• Stratum: "Willershausen Shale"; Piacenzian Stage, late Pliocene (Brauckmann *et al.* 2001)
• Remarks: This is the type species of *Stigmellites*. The form of the mine is impossible to judge from the published illustration. Only a single North American species, as yet unnamed, is known for feeding on modern Berberidaceae (see # 38). Brauckmann *et al.* (2001) observed incorrectly that Kernbach's species and generic descriptions are nomenclatorially invalid.

• # 70 *Stigmellites pliotityrella* Kernbach, 1967
Stigmella pliotityrella Kernbach, 1967: 106, fig. 4
Stigmellites pliotityrella; Kozlov 1988: 32
Stigmellites pliotityrella; Skalski 1990a: 127
Family uncertain; Brauckmann *et al.* 2001: 33
Stigmellites pliotityrellus; Sohn *et al.* 2012: 25
• Leaf mine—Host: Fagaceae: *Fagus sylvatica* L.—[1 ex.] Coll: GPUG (HT: 596–3–3050)
• Loc: Germany: Niedersachsen, Willershausen am Harz
• Stratum: "Willershausen Shale"; Piacenzian Stage, late Pliocene (Brauckmann *et al.* 2001)
• Family uncertain; Brauckmann *et al.* 2001: 33
• Remarks: See under species # 69 for the validity of Kernbach's names. Of the two extant European species of Nepticulidae feeding on *Fagus*, the mine resembles more *Stigmella hemargyrella* (Kollar) than that of *S. tityrella* (Stainton). However, we cannot place this mine firmly into *Stigmella*, since *Ectoedemia* species with relatively similar mines also are known to feed on *Fagus* (in Japan) and could have become extinct in Europe.

• # 71 Nepticulidae: *incertae sedis* multiple species (DT's)
Leaf mines; Labandeira *et al.* 2007
• Leaf mine—Host: Various angiosperm hosts—[multiple exx.] Coll: Different collections
• Loc: Numerous localities
• Stratum: Late Cretaceous, Paleogene and Neogene
• Remarks: *The Guide to Insect (and other) Damage Types on Compressed Plant Fossils* (Version 3.0) (Labandeira *et al.* 2007) documents a variety of damage types (DT's), of which several are very similar to extant Nepticulidae. In our opinion, these include DT37 (exemplar also shown in Wilf *et al.* 2001 as supplementary figure 5), DT40, DT43 (also shown in Labandeira *et al.* 2002b), DT45, DT59 (also shown in Labandeira *et al.* 2002b fig 1), DT65, DT90, DT91, DT92, DT93, DT104 and DT105. These exemplars originate from different time intervals, formations, world regions, habitats and host plants. This volume currently is being updated and is scheduled to be published in book form (Version 4.0) in a few years.

Removed from Nepticulidae

• # 72 reference to non-existing fossil
nepticulid; Grimaldi & Engel 2005: 572
putative nepticulids; Fischer 2013: 85
• Adult in amber—[1 ex.] Coll: not stated
• Loc: not stated
• Stratum: [unknown formation]; likely Santonian Stage, Late Cretaceous
• Remarks: This record potentially is the oldest nepticulid amber fossil, but offers a puzzling case. In Grimaldi & Engel (2005) it is mentioned as "a probable adult [nepticulid] in late Cretaceous Siberian Amber", for which the authors refer to the work by Skalski (pers. comm. from Prof. Engel). In reviewing Skalski's work however, including an overview of all the fossils known to the author in 1990, there is no reference to Siberian Amber nepticuloid fossils.

• # 73 Adeloidea
?Nepticulidae; Kristensen & Skalski 1998, 1998: p. 18
putative nepticulids; Fischer 2013: 85
• Adult in amber—[1 ex.] Coll: Ottawa
• Loc: not stated
• Stratum: Foremost Fm.; Campanian Stage, Late Cretaceous
• Remarks: This specimen could be the oldest nepticulid amber fossil, representing an age about twice that of Baltic Amber. However, we believe this specimen is more likely a heliozelid, or at least an adeloid in affinity. The visible veins course to the wing margin, whereas in Nepticulidae veins usually become obsolete before the margin, and the visible valvae of the male genitalia show a structure resembling a stalked pectinifer, characteristic of Adeloidea. The small size and venation suggest it could be heliozelid or closely related to that family. This fossil will be studied with x-ray techniques for further details, which will be published elsewhere. In any case, we remove the specimen herein from the nepticuloid fossil record. The fossil is dated at 72 Ma in manuscript texts that Kristensen *et al.* worked on for the publication of this fossil. [Examined by EJvN].

• # 74 Coleoptera
?Nepticulidae; Rozefelds 1988b: 77, fig. 2
?Nepticulidae; Labandeira *et al.* 1994: 12281
?Nepticulidae; Labandeira 1998: fig 2A
?Nepticulidae; Zherikhin 2002: 320
?Nepticulidae; Sohn *et al.* 2012: 27
• Leaf mine—Host: Umkomasiaceae: *Pachypteris crassa* Townrow—[1 ex.] Coll: QMSB (QMF15346)
• Loc: Australia: North Queensland, Cape York Peninsula, Cape Melville, Clack Island
• Stratum: Battle Camp Fm.; Tithonian–Berriasian Stages, Late Jurassic–Early Cretaceous boundary
• Remarks: This fossil is approximately 38 my older than any other fossil reliably assigned to Nepticulidae. The host is a corystosperm seed fern. The fossil pinnules exhibit five visible mines, of which one is poorly preserved. The mines however do not increase in width as is typical of the Nepticulidae, and are rather long, without clear frass visible. We find it much more likely that this mine is coleopteran rather than lepidopteran (see also Ding *et al.* 2014).

• # 75 Gracillariidae
Tinea araliae Fritsch, 1882: 6, pl. 2: 7
Eriocranioidea; Zherikhin 1978: 74
?Stigmellites araliae; Kozlov 1988: 30
Stigmellites araliae; Skalski 1990a: 127
Stigmellites araliae; Sohn *et al.* 2012: 24
• Leaf mine—Host: Araliaceae—[1 ex.] Coll: not stated
• Loc: Czech Republic: Bohemia, Perucher-Schichten, Vyšerovic; Bohemia, Perucher-Schichten, Lipenz

- Stratum: Perucher Fm.; Cenomanian Stage, Late Cretaceous
- Remarks: This very schematic drawing does not show much else other than a long gallery mine. This specimen is more likely to be a gracillariid mine. Since no nepticulid is known to feed on extant Araliaceae, but several Gracillariidae do feed on this plant-host family, particularly the genus *Eumetriochroa* Kumata, with mines similar to *Phyllocnistis* (Kobayashi *et al.* 2011). We tentatively remove this species from Nepticulidae.

• # 76 Undetermined

Galleries; Berry 1916: 32, pl. 23: 3, pl. 31: 1, 3, pl. 38: 4, pl. 39, pl. 92.
Nepticulidae; Sohn *et al.* 2012: 26

- Leaf mine—[multiple exx.] Coll: not stated
- Loc: Various localities in the Mississippi Embayment.
- Stratum: not reported
- Remarks: This specimen was incorrectly put in the same record as # 38 by Sohn *et al.* (2012). Here, the record is excluded from Nepticulidae. In this one case it is unclear if the material represents leaf mines or other types of damage.

• # 77 *Foliofossor cranei* Jarzembowski, 1989

Mine type 3; Crane & Jarzembowski 1980: 663, fig 10
?Nepticulidae; Kozlov 1988: 30
Foliofossor cranei Jarzembowski, 1989: 448
Stigmella sp.; Skalski 1990a: 127

- Leaf mine—Host: Platanaceae: *Platanus schimperi* (Heer) Saporta & Marrion—Coll: BMNH HT (In. 64550)
- Loc: United Kingdom: Cold Ash, or Newbury, Berkshire (N 51° 22' W 1° 17').
- Stratum: Reading Fm.; late Paleocene, Priabonian Stage
- Remarks: Jarzembowski (1989) doubts the assignment of this leaf mine to a particular insect taxonomic order, and provides an ichnogenus name. Crane & Jarzembowski (1980) consider it to be a dipteran mine, but Kozlov (1988) assigns it to Nepticulidae. There is a certain resemblance of this mine to extant *Stigmellites tyshchenkoi* that also feeds on *Platanus*, but the fossil mine is significantly older by approximately 40 my. We believe that assignment to Nepticulidae is unlikely.

• # 78 *Troponoma festunata* Krassilov, 2008

cf. Stigmella; Krassilov 2008a: 265, fig. 3a, b
Troponoma festunata Krassilov, 2008b: 102, PL XXXVI figs. 1–3

- Leaf mine—Host: Family unknown: *Dewalquea gerofitica* (Dobruskina) Krassilov—[several exx. on one leaf] Coll: IEUH (HT IG1–1001)
- Loc: Israel: southern Negev, Gerofit
- Stratum: Ora Fm.; mid-Turonian Stage, Late Cretaceous
- Remarks: Krassilov (2008b) mentions that "similar mine configurations are known in *Stigmella*, Nepticulidae, although radially spreading festoons (sensu Hering 1951) may indicate a gracillariid miner similar in habit to the digitate mines of *Parectopa robiniella*". In Krassilov (2008a) this record is referred to as a *Stigmella*-type track. We fail to recognize any nepticulid characteristics in these leaf mine fossils and rather doubt if they actually represent leaf mines.

• # 79 *Troponoma curvitracta* Krassilov, 2008

Troponoma curvitracta Krassilov, 2008b: 101, Pl. VI fig 4b, Pl. XXX fig. 1; Pl. XXXV figs. 1–5

- Leaf mine—Host: Family unknown: *Dewalquea gerofitica* (Dobruskina) Krassilov—[>4 exx.] Coll: IEUH (HT IG1–160)
- Loc: Israel: southern Negev, Gerofit
- Stratum: mid-Turonian Stage, Late Cretaceous
- Remarks: Krassilov (2008b) states that "The mine configurations of th[is] kind are sometimes produced by *Stigmella*. However, egg persistence on mines is a feature typically of coleopteronomes, and comparable looping mines are made by a weevil *Rhamphus pulicarius* (Herbst) on *Betula* (cf. Hering)". From the photographs it is

difficult to judge if there is an egg-like structure visible, but if there is, this would be a character also typical for Nepticulidae. As in the case for record # 78, we do not recognize sufficiently relevant characters in these images to attribute this fossil to Nepticulidae.

An overview of the data

A summary of the age intervals of the 69 fossil Nepticulidae records for which age estimates are available is provided in Fig. 21. Records 1–11 are adult fossils, records 12–72 represent leaf mine records. From the late Early Cretaceous onwards, there are episodic occurrences of leaf-mine fossils attributed to Nepticulidae. Based on our checklist, the oldest nepticulid fossils are records #12–17, which were also mentioned 16 years ago by Kristensen and Skalski (1998) as the likely oldest records, currently dated at 102 Ma. Table 1 shows an overview of the variously identified plant-host families from which fossil nepticulid leaf mines have been recorded throughout geological record. Table 1 also provides the extant genera that occur as leaf miners on those fossil host-plant families.

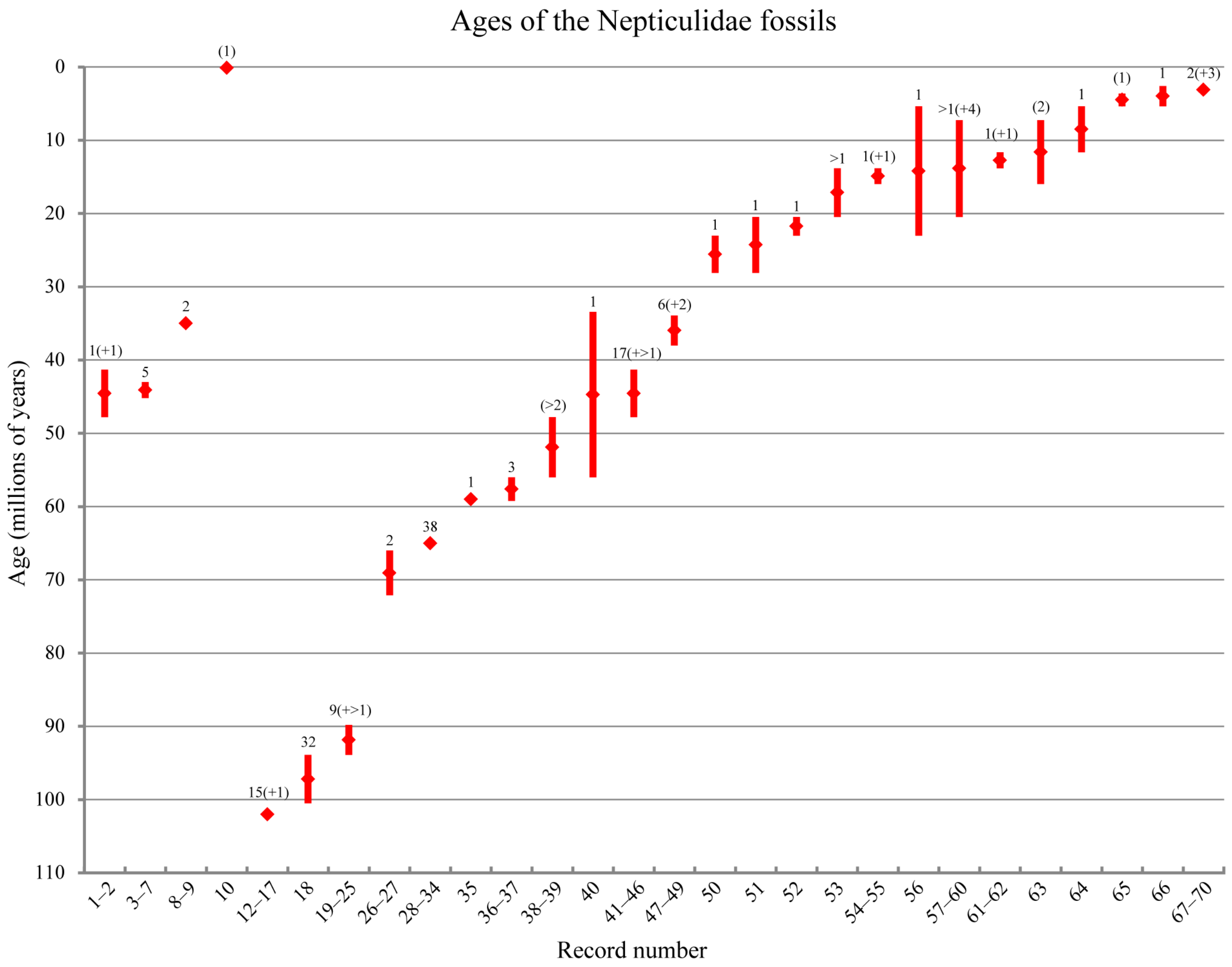

FIGURE 21. Geochronologically ranked age intervals corresponding to literature-mentioned ages for the 69 fossil records of Nepticuloidea that have documented geochronologic ages. Entries 1–10, at the upper-left, represent body-fossil occurrences; entries 12–70, forming the linear series from lower-left to upper-right, are leaf miners. Fossil record numbers refer to those in the checklist. The number of exemplars involved for each datapoint is indicated above the range, numbers between parentheses indicate unverified or uncertain identifications. The ">" sign indicates that there was no exact number of exemplars provided. For cases where a subjective indication was given within an epoch, such as Late Priabonian, this is shown spanning the entire Priabonian Stage. Stage-level boundaries are from Ogg *et al.* (2008).

TABLE 1. The geochronologic distribution of host-plant families identified from fossil Nepticulidae leaf mines and the extant nepticulid genera that occur on those host plant families, arranged by systematic plant order (APG III 2009). The Stage level boundaries follow Ogg *et al.* (2008).

Higher Angiosperm group	**Order**	**Host family**	**Record #'s**	**Early Cretaceous** 145.0–100.5 mya	**Late Cretaceous** 100.5–66.0 mya	**Paleocene** 66.0–56.0 mya	**Eocene** 56.0–33.9 mya	**Oligocene** 33.9–23.0 mya	**Miocene** 23.0–5.3 mya	**Pliocene** 5.3–2.6 mya	**Pleistocene** 2.6–0.01 mya	**Extant genera on host family**
Angiosperms			18, 45, 15, 71	+	+		+					
Pre-Magnoliid	Austrobaileyales	Schisandraceae	53						+			No
Magnoliids	Laurales		16, 13	+								No
Magnoliids	Laurales	Lauraceae	52, 49				+		+			No
Eudicots			46, 36, 41, 34, 14, 39, 47, 38			+	+					
Eudicots	Ranunculales	Berberidaceae	54, 69						+	+		*Stigmella*
Eudicots	Proteales	Platanaceae	12, 20, 23, 28	+	+	+						*Acalyptris, Ectoedemia*
Eudicots	Trochodendrales	Trochodendraceae	30			+						No, but not searched
Core Eudicots	Saxifragales	Cercidiphyllaceae	19, 21, 22, 27, 31, 35		+	+						No, but not searched
Rosids	Myrtales or Malpighiales		24		+							*Stigmella, Ectoedemia* on Malpighiales, *Pectinivalva, Acalyptris* on Myrtales
Rosids	Malpighiales	Salicaceae	32			+						*Stigmella, Ectoedemia*
Rosids	Rosales	Rhamnaceae	30			+						*Stigmella, Acalyptris, Ectoedemia*
Fabids	Oxalidales	Elaeocarpaceae	48				+					*Roscidotoga*

……*continued on the next page*

TABLE 1. (Continued)

Higher Angiosperm group	Order	Host family	Record #'s	**Early Cretaceous** 145.0–100.5 mya	**Late Cretaceous** 100.5–66.0 mya	**Paleocene** 66.0–56.0 mya	**Eocene** 56.0–33.9 mya	**Oligocene** 33.9–23.0 mya	**Miocene** 23.0–5.3 mya	**Pliocene** 5.3–2.6 mya	**Pleistocene** 2.6–0.01 mya	Extant genera on host family
Fabids	Fabales	Fabaceae	40				+					*Stigmella, Acalyptris, Trifurcula*
Fabids	Fabales	?Fabaceae	37			+						*Stigmella, Acalyptris, Trifurcula*
Fabids	Fagales	Betulaceae	67, 64						+	+		*Stigmella, Bohemannia, Ectoedemia*
Fabids	Fagales	Fagaceae	56, 57, 70, 55, 61, 65, 58, 63, 62						+	+		*Stigmella, Ectoedemia*
Fabids	Fagales	Juglandaceae	50, 29			+		+				*Stigmella, Ectoedemia*
Fabids	Rosales	Moraceae	43				+					*Stigmella*
Fabids	Rosales	Ulmaceae	66, 68							+		*Stigmella, Ectoedemia*
Fabids	Rosales	Rosaceae	26, 42		+		+					*Stigmella, Areticulata, Trifurcula, Bohemannia, Ectoedemia*
Malvids	Sapindales		15, 17	+								*Stigmella, Ectoedemia, Acalyptris, Trifurcula*
Asterids	Cornales	Cornaceae	33			+						*Acalyptris, Ectoedemia*
Asterids	Ericales	Symplocaceae	51					+	+			*Acalyptris*

Discussion

The checklist presented herein for fossil Nepticulidae contains 71 records, of which 55 were re-examined by us and the remaining records were judged for plausibility. The records often include multiple exemplars or taxa presented as a single record. The checklist spans publications from 1862 to 2014, a period of time during which the systematics of Nepticulidae changed considerably (van Nieukerken *et al.* 2011b; Hoare 2000; van Nieukerken 1986). The identifications in the checklist have been updated to match recent systematic results and insights. The analogy of many fossil leaf mines with the extant genus *Stigmella* is expected, as *Stigmella* is among the most species-rich genus with the most variable leaf mine types and varied spectrum of hosts within the Lepidoptera. Our designations have been conservative; we assign only a few relatively recent leaf-mine fossils on known host plants to the modern genus *Stigmella* and a single Australian mine tentatively to the Australian endemic genus *Roscidotoga*. Leaf mines predominantly represent behavioural characters and, although generally recognized as useful for identification, have never been analysed within a phylogenetic context. Consequently, assignment of fossil leaf mines to lower-level extant groups is precarious. However, when there is use of a combination of characters, assignments to many groups often can be excluded and a fairly certain identification usually is feasible. Such reliably identified assignments of fossil leaf mines constitute an important addition of data, compared to the scarce inventory of adult fossils. As a result, fossil leaf-mine assignments allow for a more reliable perspective regarding the estimated age of the family.

Classifying fossil material. The classification of fossil adult specimens usually is straightforward. Extant species and groups have been erected based on (syn)apomorphic characters of the adults and using those characters that allow identification of fossil material to the lowest taxonomic rank, as provided by the available characters. There often is one or, at most, a few, exemplars that frequently result in each new record as a new (ichno)species. For fossil insect leaf mines, the best approach for classifying the material frequently is less straightforward. This indecisiveness in assignment is attributable often to dozens to hundreds of specimens that have been examined, and assignment of species and erecting new species for all leaf-mined foliar assemblages becomes a daunting task. Historically, three different approaches linked to different purposes have been used to systematize leaf-mined foliar assemblages, discussed in Scott and Titchener (1999). They are 1), comparative and functional morphology; 2), comparative analogy; and 3), ichnotaxonomy. The Nepticulidae checklist provides examples from all three categories. Certain authors have generally favoured ichnotaxonomic procedures (Kozlov 1988; Krassilov 2008b), and among other authors there appears to be a historical transition from comparative analogy up to the mid-1990's (Opler 1973; Stephenson 1991), towards a comparative and functional morphological approach in more recent studies (Donovan *et al.* 2014; Knor *et al.* 2012).

Comparative and functional morphology is the most conservative approach and prevents unjustified assignment of fossils to extant groups. However, checklists such as the one presented here would be better facilitated if analogies to modern taxa are clearly stated in the primary literature. A single, complete overview of all possible herbivore candidates and their typical characteristics is not yet available (but see Ding *et al.* [2014] for an example from the Coleoptera). Hering's published work (Hering 1951; Hering 1957) has commonly been used as a conventional source on leaf-mine types and for analogies with modern taxa, but it has a strong European bias and is out-of-date. Especially in the subtropical and tropical regions, there are many aberrant and overlapping leaf-mine morphologies for various leaf-mining groups. The European leaf miner website with keys and descriptions to all leaf miners of Europe, replete with abundant images, can be a useful starting point to grasp the diversity of a broad spectrum of leaf-mining groups (Ellis 2014). However, as this site applies to Europe only, it has limitations to extralimital leaf-mine material. The web-documented guide for fossil leaf mine and other insect-caused fossil plant damage types (Labandeira *et al.* 2007) commonly has been used in recent studies, but does not provide links to analogous extant groups. (The next version of the *Damage Guide* will have links to modern analogous groups for each mining and non-mining damage type (DT), many of which will be new.) These links for lepidopteran and other types of distinctive fossil mines will follow a similar format such as those published for dipteran Agromyzidae (Winkler *et al.* 2010) and those presented here for lepidopteran Nepticulidae. Such an improvement hopefully will enable additional commentary regarding the essential characters available for reliable identifications. When publishing fossils in general, references to collections are invaluable in allowing for further study. When stating leaf-mine analogies, the scope of the reference material should be clearly indicated.

In cases where identification to family can be made, we advocate the use of an ichnogenus to describe species from fossil leaf mines. Each leaf-mine ichnogenus also would be represented by a damage-type synonym, or DT number, for the assessment of herbivory (Labandeira *et al.* 2007), allowing for quantitative analyses (e.g. Labandeira *et al.* 2002; Wilf *et al.* 2005; Donovan *et al.* 2014). When compiling the checklist, it became clear that many fossils have been mentioned or depicted in multiple publications, for which, from our thorough study of the texts and images, it became necessary to link the publications to the same leaf-mine record. In the checklist we have resorted to numbering the records, but allowance for cross-publication links is the most sustainable option for assignment of a species name to a fossil.

It should also be noted that when the fossil cannot be linked to any extant family, the value of ichnotaxonomy quickly deteriorates and devolves to a parallel naming system. This is exemplified by the work of Krassilov and colleagues (Krassilov 2008b). From remarks in the figure captions of this work, we were able to notice that the authors did recognize analogies to extant Nepticulidae; fossils were described as species within genera without higher taxonomic ranking or an indication of affiliation. Consequently, such groups cannot be linked to any modern lineage. We believe that this approach fails to advance any of the purposes for studying nepticulid fossil herbivory, and a preferable approach would be to use either comparative and functional morphology, or alternatively and better yet, use an ichnotaxonomic system such as the damage-type system, with a goal toward recognizing characteristic analogies to better place the fossils in modern groups whenever possible. However, there is one significant exception. In the older part of the geological record where Nepticulidae are absent, such as the later Paleozoic to the mid Mesozoic, all to most of insect-mediated damage, including Triassic and Jurassic leaf mines, may lack links to modern herbivorous taxa, and instead represent extinct groups of herbivores. Under these conditions the best option is to use the parallel ichnotaxonomy of the DT system (Labandeira *et al.* 2007), in which a more functional and morphological perspective is used (e.g., Schachat *et al.* 2014).

Age of Nepticulidae. Although it is difficult to assign some of the leaf-mine fossils with complete certainty to Nepticulidae, it seems unlikely that the overwhelming majority of the records would not be assigned to Nepticulidae. In addition, it is highly probable that nepticulid leaf-mine fossils date to the late Albian of the Early Cretaceous, at 102 Ma (Fig. 21). Molecular dating of Lepidoptera phylogeny by Wahlberg *et al.* (2013) estimated the split between Nepticulidae and Opostegidae between 100 and 130 Ma (95% confidence interval). Their study used seven calibration points throughout Lepidoptera, and also included the nepticulid fossil record # 12. Accidentally, Wahlberg (pers. comm.), used record # 12 to calibrate the split between *Ectoedemia* and *Opostega* at 120 ± 10 Ma, whereas the actual age of the referenced material is estimated at 102 Ma. Without the nepticulid calibration point, and reliance instead only on the remaining six calibration points, the estimated molecular-phylogenetic age range of Nepticulidae is increased to 75–150 Ma. Wilf and Escapa (2014) provide a compelling demonstration of this phenomenon from the fossil records of several land-plant lineages.

Host plant relationships. Table 1 lists the host plants of fossil Nepticulidae that have been identified, according to the approximate taxonomic order of the Angiosperm Phylogeny Group (APG III 2009). After excluding the corystosperm seed fern fossil, which we judged to be non-nepticulid, only angiosperms evidently hosted nepticulids in the fossil record. Of these, six are non-eudicot (Laurales for records # 13, 16, 49, 52; Austrobaileyales for # 53); there are no extant Nepticulidae known to feed on these host orders. Angiosperms have been estimated based on molecularly dated phylogenies to have originated during the Triassic or Jurassic, at 193 Ma, although their empirical fossil record begins in the mid Early Cretaceous (Valanginian Stage), which is probably closer to the accurate date for the true origin of the angiosperms (Friis *et al.* 2011). The principal eudicot radiation began during the mid Early Cretaceous, and intensified to the mid Cretaceous (Magallón *et al.* 2013). Nepticulidae fossils from the Cretaceous have been found on Laurales, Proteales, Saxifragales, and several plant species for which an ordinal placement is uncertain. Nevertheless, these basal angiosperm host lineages indicate that they were the dominant plant groups during the mid Cretaceous, as evidenced by their general abundance in the mid Early Cretaceous to Early Paleogene fossil record (Graham 1999). Platanaceae in particular were a common and diverse group during the Late Cretaceous and Paleogene (Johnson 1996; Graham 1999; Friis *et al.* 2011), and formed a major plant-host family for insect herbivores (Labandeira *et al.* 1994, Labandeira, 1998). This perhaps explains the common occurrence of Nepticulidae leaf mines from the Dakota Formation (102 Ma, records #12–18), which likely represent multiple species and are most abundant on *Platanus* and other Platanaceae. Dakota-age leaf mines also are found on several other, unrelated, non-dicot hosts. Leaf-mine fossils approximately 10 my younger, from Kazakhstan, are also diverse (# 19–23), and include *Platanus* and related genera as hosts (# 20, 23). Additionally important associations include the leaf genera *Trochodendroides* (not to be confused with

Trochodendron in the Trochodendraceae) (records # 19, 21, 22), and *Cercidiphyllum* in the Cercidiphyllaceae (records # 19, 21, 22, 27, 31, 35), associated with fruits of the genera *Nyssidium* and *Joffrea* (Friis *et al.* 2011). The Cercidiphyllaceae forms a basal clade of the Saxifragales, occurring in floras during the Late Cretaceous and into the Paleogene from Eurasia and North-America. Modern Cercidiphyllaceae consist of two relict species in north-eastern Asia (Stevens 2013), and currently are unknown as host plants for extant Nepticuloidea. However, the modern record also reflects an absence of serious sampling. A few modern nepticulids do occur on other related host-plant lineages of Saxifragales, such as the families Altingiaceae and Hamamelidaceae. The host-plant records from combined Cretaceous occurrences suggest that Nepticulidae at that time were widespread and already had diversified onto a variety of host families across several major angiosperm lineages.

Given the time interval when likely Nepticulidae are first encountered in the fossil record, and taking into account the varied biogeographic dispersal patterns and physiognomic forms of their plant hosts, we find that an Albian to Aptian origin of the Nepticulidae is most likely, ranging from 125 to 100 m.yr. ago. This period of time also is the same interval during which dominant, woody angiosperm lineages diversified. We expect that much of the deep-time diversity of nepticulid taxa reflected in the fossil record is extinct, as are their plant hosts. One major cause of the extirpation of nepticulid leaf miners was the mass extinction event at the end of the Cretaceous (Labandeira *et al.* 2002), the Cretaceous–Paleogene boundary, which disproportionately affected some plant hosts over others (Johnson 2002). In addition, there is increasing evidence that the diversity of specialized insect herbivores was also heavily and negatively affected (Donovan *et al.* 2014; Heikkilä *et al.* 2012; Labandeira *et al.* 2002). By additional examination of the phylogeny and diversification of Nepticulidae and combining such studies with insights from the fossil record, a clearer picture of the evolutionary history of the family should emerge.

Conclusions

If we would rely on amber body fossils alone, the oldest Nepticulidae representatives would lie between 43 and 45.2 Ma, more than 60 my younger than the estimated age of the family if fossil leaf mines are included. When molecular dating is applied to a phylogeny of Lepidoptera, this young date is extended by a factor of 2.7, to 120 Ma. The identifications of leaf-mine fossils may be less precise, but because of their large numbers and their representation in the older fossil record, they nevertheless represent an undeniably important source of data, especially when classified in a way that allows them, when possible, to be assigned to extant groups. Nepticulidae currently constitute a substantial part of the biodiversity of leaf-mining insects globally, and the checklist provided herein suggests that this likely has been the case for the past tens of millions of years. The potential for assigning adult fossils to extant genera however, makes continued search for amber-entombed Nepticulidae also important (Labandeira 2014). There is promising material in older ambers, such as Cedar Lake (Canadian) Amber (Campanian; 72–83 Ma) or Raritan (New Jersey) Amber (Turonian and Cenomanian; 89–101 Ma), of which rare lepidopteran fossils are known but generally unstudied (Grimaldi & Nascimbene 2010; McKellar & Wolfe 2010).

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Text Box: Leaf-mine terminology

Since there is a confusion regarding descriptive terms for leaf mines, and differences exist between North American and European literature, we provide a short list of terms and their synonyms. Hering (1951) provided several Latinized terms, listed below, but these versions are rarely used.

Ophionome – linear mine. A mine in which the larva moves in one forward direction. In British literature such a mine is usually termed a "gallery"; in North American literature an approximate equivalent is a "serpentine mine". The latter usage is confusing (see below). The ophionome mine is the common type in the Nepticulidae.

Heliconome – serpentine mine (auct. Hering). A linear mine that has a sinusoidal, occasionally spiral, trajectory in a leaf, particularly in its earlier stages and often later becomes a more rectilinear mine. Examples in Nepticulidae include *Enteucha acetosae* (Stainton), *Stigmella prunifoliella* (Clemens) and several *Ectoedemia* species.

Visceronome – intestinally coiled mine. A linear mine that turns back and forth in a tight, zigzag pattern, such that the individual coils are adjacent to one another in an intestine-like fashion. Example: *Stigmella viscerella* (Stainton)

Stigmatonome – blotch mine. A mine in which the larva consumes one or more tissue layers in all or several directions. Stigmatonomes are divided into two types:

Orthogenous stigmatonome. A blotch mine in which the larva consumes tissue in all directions without any preferential feeding pattern. Orthogenous stigmatonomes are rare in Nepticulidae; examples include *Ectoedemia occultella* (Linnaeus) and *Stigmella paradoxa* (Frey).

Ophiogenous stigmatonome. or a false blotch. A blotch mine originating by coalescence of linear mines, such that the larva changes feeding direction and creates the appearance of a blotch mine by an abundance criss-crossing intersections with occasional islands of unmined, often squarish, tissue. Ophiogenous stigmatonomes are more common in Agromyzidae. In Nepticulidae false blotches are often formed when the larva lacks sufficient mining space and is obliged to follow previously made mine tracks.

Ophistigmatonome – linear-blotch mine. A combination of mine types wherein the larva initiates a gallery mine, and frequently after the last molt starts the formation of a blotch, often in the form of a wide, broad gallery. Ophistigmatonomes are common in Nepticulidae, particularly in *Ectoedemia*. If the entire leaf or other foliage organ is mined, Hering (1951) has termed such a construction as a "pantonome".

Additional terms that describe mines that do not occur in Nepticulidae are: *asteronome*, star-shaped mine of radiating mine trails; *physonome*, a blister mine; and *ptychonome*, a tentiform mine. Additional terminology for mines in plant parts other than foliage are: *carponome*, occurring in fruit; *caulonome*, occurring in a stem; and *anthonome*, occurring in a flower.