NEW RECORDS AND ICHNOSPECIES OF LINEAR LEAF MINES FROM THE LATE MIOCENE-PLIOCENE FROM ARGENTINA AND THE ESTABLISHMENT OF LEAF-MINING ICHNOTAXOBASES

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Abstract. The ichnospecies *Cuniculonomus parallelus* Givulescu, 1984 and *Stigmellites serpentina* Kozlov, 1988 are recorded for the first time in Argentina and the new ichnospecies *Cuniculonomus saltensis* n. ichnosp., *Stigmellites vitatus* n. ichnosp. and *Stigmellites pervenae* n. ichnosp. are defined from two Miocene localities: Peñas Blancas and Quebrada del Horno, from northwestern Argentina. A set of characters to identify fossil linear mines is provided as well as five ichnotaxobases to differentiate the ichnogenera *Cuniculonomus*, *Stigmellites* and *Phytomyzites*. Two ichnospecies are now revised and included in *Phytomyzites: P. arcuata* (Krassilov, 2008a) comb. nov. (*Ophionoma*) and *P. crucitracta* (Krassilov, 2008a) comb. nov. (*Troponoma*). Finally, a review of fossil record of linear mines is provided.

INTRODUCTION

Leaf mines are endophytic interactions, caused by insect larvae which excavate tunnels within the parenchyma, epidermis or other internal tissues of leaves but leaving intact the outer cell layers (Hering 1951). Leaf-miner species are known in the orders Lepidoptera, Diptera, Coleoptera and Hymenoptera (Needham et al. 1928; Hering 1951). The three basic morphotypes of mines are linear, blotch and trumpet types-shaped, the latter being a combination of the two first ones (Needham et al. 1928). Although these three shapes are known on fossil leaves (Labandeira et al. 2007), linear mines are the oldest and have the broader record. Most linear mines described in the fossil record have been assigned to Lepidoptera, especially the family Nepticulidae (Kozlov 1988; Sohn et al. 2012; Donovan et al. 2014; Doorenweerd et al. 2015), and to a lesser extent to Agromyzidae (Diptera) (Straus 1977; Winkler et al. 2010).

Demonstrable linear mines are known since the Triassic (Rozefelds 1985; Rozefelds & Sobbe 1987; Zherikhin 2002; Scott et al. 2004; Labandeira

2006; Krassilov & Karasev 2008) and their records are increasing throughout the Mesozoic and the Cenozoic (Hickey & Hodges 1975; Liebhold et al. 1982; Kuroko 1987; Scott et al. 1992; Labandeira et al. 1994; Labandeira 1998; Krassilov 2007; Krassilov & Shuklina 2008; Donovan et al. 2014). Most of these records come from the Northern Hemisphere, mainly Europe and USA (Opler 1973, 1982; Lang et al. 1995; Krassilov 2008a; Wappler et al. 2009; Wappler 2010). In South America, Adami-Rodrigues et al. (2011) described a linear mine of nepticulid origin, in a gymnosperm leaf from the Triassic of Brazil. Martins-Neto (1989) reported the ichnospecies *Nepticula? almeidae* on cf. *Symplocos* (Symplocaceae) from the Oligocene from the southern of Brazil. Horn et al. (2011) described linear mines in *Malvaciphyllum quenquiadensis* (Malvaceae) from the middle Miocene and *Nectandra saltensis* (Lauraceae) from the late Miocene of northwestern Argentina.

In recent decades, ichnotaxonomy has assumed a leading role in the study of fossil plant-insect associations. In particular, the ichnotaxonomy of linear leaf mines has been better developed compared with other plant-insect damages (see Appendix). Historically, many ichnotaxa were named according to the inferred producer, contrary to the princi-
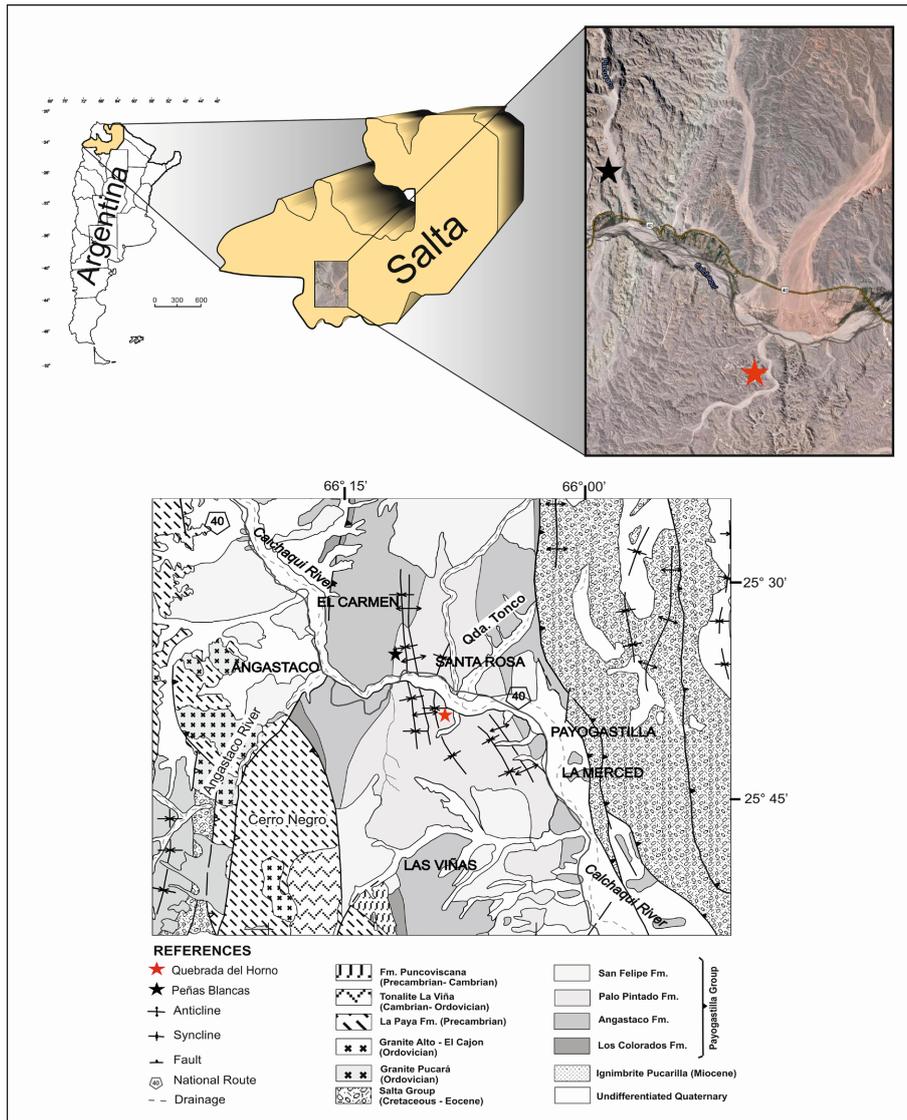
Fig. 1 - Map showing the fossil localities of Peñas Blancas and Quebrada del Horno (edited from Galli et al. 2011).

ples of ichnotaxonomy. In addition, the diagnosis of most ichnotaxa are incomplete and lack relevant characters. Examples include the ichnogenera *Nepticula*, *Tinea*, *Stigmellites* and *Phytomyzites* (von Heyden 1862; Fritsch 1882; Kernbach 1962; Straus 1977; Givulescu 1984; Koslov 1988; Jarzembowski 1989; Martins-Neto 1989). These designations differ from those of other authors who have considered only morphological characters of fossil mines for nomenclature, such as *Cuniculonomus* and *Foliofossor* reported by Straus (1977) and Jarzembowski (1989) respectively. The ichnogenus *Phytomyzites* is unique in having a diagnosis based only on morphological characters, which provides useful characters for comparison to other ichnogenera. However, the diagnosis of the two other ichnogenera described here (*Cuniculonomus* and *Stigmellites*) include interpretative attributions circunscribing the inferred producer insect, which are

consider inappropriate in the ichnotaxonomical nomenclature (Kelly 1990; Bertling et al. 2006). Despite numerous studies focused in ichnotaxonomy of fossil mines, there is a confusion in several aspects, including inconsistencies in diagnosis mentioned above. For this reason, it is important to establish solid criteria to define ichnotaxa based on the ichnotaxonomical principles.

The objectives of this report are: 1) to describe the three new ichnospecies of linear leaf mines of *Cuniculonomus saltensis* n. ichnosp., *Stigmellites vitatus* n. ichnosp., and *Stigmellites pervenae* n. ichnosp.; 2) to document for the first time the ichnospecies *Cuniculonomus parallelus* and *Stigmellites serpentina* from the late Miocene of Argentina; and 3) to propose a set of morphological characters to differentiate the ichnogenera *Cuniculonomus*, *Stigmellites* and *Phytomyzites* for linear leaf mines.

Character sets used in the identification and ichnotaxonomy of fossil linear mines

Oviposition: The oviposition site is located anywhere on the leaf. Scarring around the ovipositions can be present or not. The shape varying from circular to lenticular (Winkler et al. 2010). Ovipositions can be single or are associated to circular puncture marks (Winkler et al. 2010; Jud & Sohn 2016).

Course: Linear mines show different degrees of sinuosity; there are mines with several shifts in sinuosity and frequency, resulting in a trajectory that is nearly straight or slightly sinuous (Givulescu 1984; Lewis 1969). Those that are more sinuous, are named "serpentine mines" and include two other types; "heliconoma" (highly sinuous, sometimes they are thick and highly coiled in the proximal section) and "visceronoma" (intestiniform mines) (Doorenweerd et al. 2015).

Position in the leaf: Mines can be deployed anywhere in the foliar lamina; some mines cross the primary vein (Wappler & Denk 2011), whereas others are limited to one half of a lamina delimited by a midvein and the lamina margin (Kuroko 1987; Hickey & Hodges 1975) or even enclosed between two secondary veins (Peñalver & Delclòs 2004; Paik et al. 2012).

Size: Leaf mine size is highly variable; as fossil mines range from 5 mm (Winkler et al. 2010) to 10 cm in length (Lang et al. 1995). Occasionally, the gallery width can be constant throughout the entire leaf-mine trajectory (Givulescu 1984; Kozlov 1988) or alternatively increase several times the original size (Lang et al. 1995; Crane & Jarzembowski 1980). Many leaf mines start up as linear or serpentine during the early and middle instars and end up as a blotch during last instar. This involve the ontogenetic phenomenon of hypermetamorphosis (Labandeira et al. 1994).

Coprolites (shape and disposition): Some leaf miners consume solid (cellular) tissue, depositing spheroidal, ellipsoidal or thread-like fecal pellets (Donovan et al. 2014). Other leaf-mining taxa consume protoplasts and other plant fluids leaving excreta with splatter-like or sometimes the coprolite has a fluid consistency (Winkler et al. 2010). Coprolite distribution is variable. However, some coprolite trajectories can be primarily continuous and are interrupted only where the mine crosses a major vein (Crane & Jarzembowski 1980). Other leaf mines have discontinuous trajectories with interruptions within the galleries lacking frass deposition (Krassilov 2008a). By contrast, coprolite may be arranged in center of a gallery (Kozlov 1988), or alternating between the two sides of the mine (Winkler et al. 2010). Sometimes there is no evidence of discernable coprolites or they are absent (Jarzembowski 1989; Lang et al. 1995), although this could be attributed to inconspicuous fluidized fecal material from a sap-feeding larva.

Terminal chamber: This section frequently has not coprolites (Crane & Jarzembowski 1980); terminal chamber is circular or roughly rectangular (Stephenson 1991; Winkler et al. 2010). Some specimens have undeveloped terminal chamber (Givulescu 1984; Lang et al. 1995; Krassilov 2008b). However, the terminal chamber, often a pupation site can be modified with a slit ovoidal hole enlarged gall-like structure, an excised pupal case that descends to the ground, on other modifications (Needham et al. 1928; Hering 1951).

GEOLOGICAL SETTING

The Palo Pintado Formation is located in the southern of Salta Province, Argentina. It crops out on both borders of the Calchaquí River, between 25º41'01"S – 66º07'55"W and 25º40'59"S – 66º05'49"W (Galli et al. 2011) (Fig. 1). This formation has a stratigraphic section of 1200 m, and forms part of the Payogastilla Group, intercalated between the Angastaco above and the San Felipe Formations below. Lithologically, The Palo Pintado Fm. is principally composed by sandstones alternating with siltstones and to a lesser conglomerates. Sandstones present a brownish coloration while siltstones exhibit yellow and brown hues that merge to greenish sediments. Throughout the section there is disposition in successive finer-grained sedimentary cycles, interpreted as resulting from anastomos rivers of low rank and entrainment (Díaz 1985, 1987; Díaz et al. 1987; Herbst et al. 1987; Anzótegui 1998, 2006). The assigned age of these deposits is estimated between 10.29 ± 0.11 Ma. (K/Ar) (Galli et al. 2008) and 5.27+- 0.28 Ma. (U-Pb method on zircon) (Coutand et al. 2006). The leaf impressions originate from the basal section of the formation at the Peñas Blancas (25º40'15"S – 66º05'80"W) and Quebrada
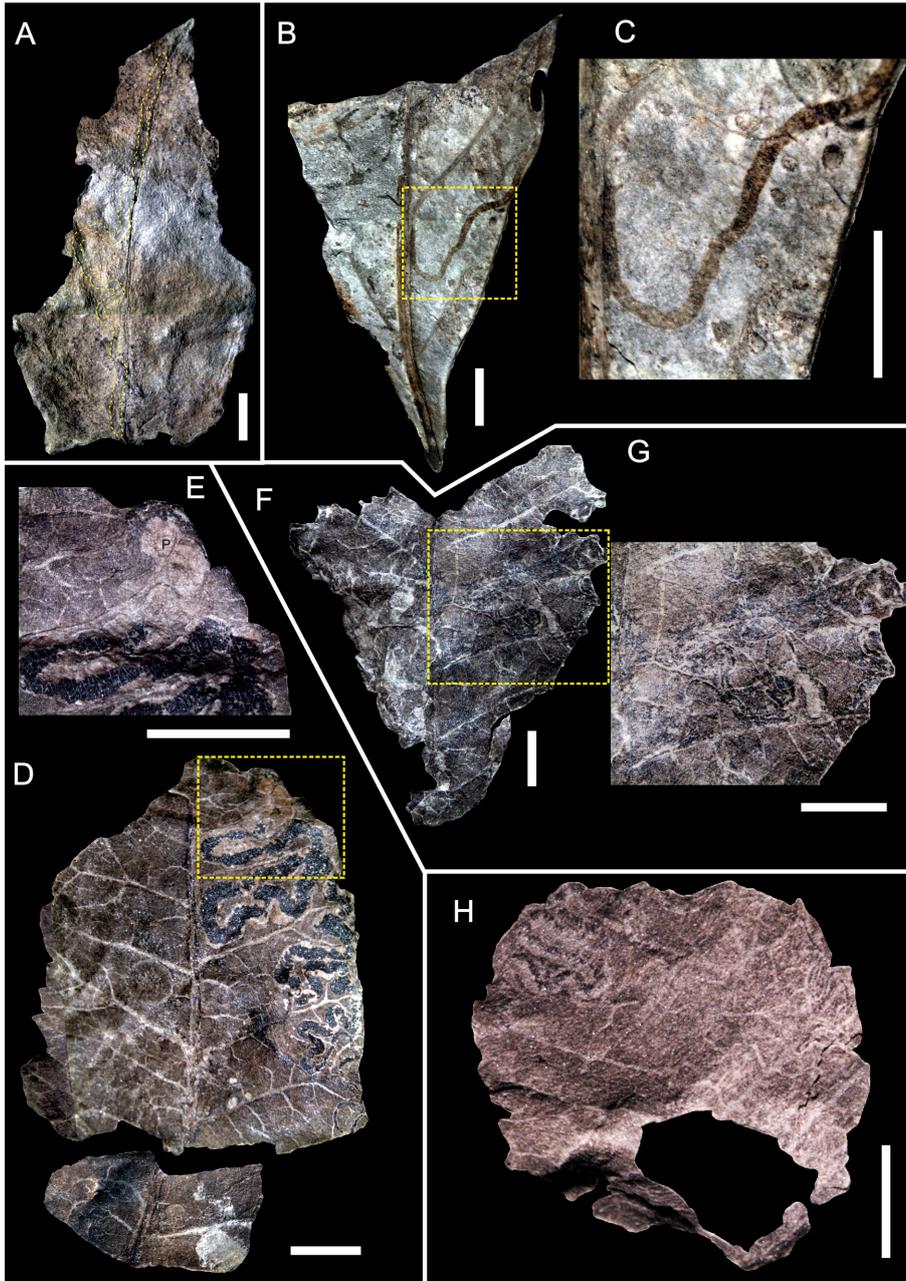
Fig. 2 - A) *Cuniculonomus parallelus* (Givulescu, 1984), a yellow dotted line delimits the linear mine; B) *Cuniculonomus saltensis* n. ichnosp., the mine shows a brownish coloration, which differentiates it from the rest of the leaf; C) detail of B, the image shows the initial and central portion of the mine; D) *Stigmellites vitatus* n. ichnosp., a complete mine entirely developed within one half-leaf element; E) detail of D, showing the terminal chamber and the exit hole (p); F) *Stigmellites serpentina* (Kozlov, 1988), showing serpentine mines is arranged between two secondary veins; G) detail of F; G) *Stigmellites pervenae* n. ichnosp.; this mine is developed on both half-leaf elements. Bar scale= 3 mm.

del Horno (25°42'41"S – 66° 03'45"W) localities. The paleoenvironmental context was inferred from fossil plants, where humid-wet communities predominate, with few representatives of xeric environments. The fossil deposit denotes a warm and wet climate with minimal seasonality (Anzótegui 2006; Mautino 2010).

SYSTEMATIC DESCRIPTION

Subgroup **Phagophytichnida**
Ichnofamily Paleominidae Vialov, 1975
Ichnogenus *Cuniculonomus* Straus, 1977

Type ichnospecies: *Cuniculonomus carpini* Straus, 1977

Emended diagnosis. Linear mines usually maintaining the same width of the gallery in its entire course or occasionally a slightly widening at the terminal section is observed.

Remarks. The diagnosis of *Cuniculonomus* established by Straus (1977) is emended here because the original erection of the ichnogenus lacks the appropriate characters to differentiate this ichnogenus from other linear mines as *Stigmellites* and *Phytomyzites*. Straus (1977) only defined *Cuniculonomus* as a mine found on an angiosperm leaf that was made by an unknown insect.

Fig. 3 - Schemes of the ichnospecies described in this work. A) *Cuniculonomus parallelus*; B) *Cuniculonomus saltensis* n. ichnosp.; C) *Stigmellites serpentina*; D) *Stigmellites vitatus* n. ichnosp.; E) *Stigmellites pervenae* n. ichnosp. Scale bar = 3 mm.
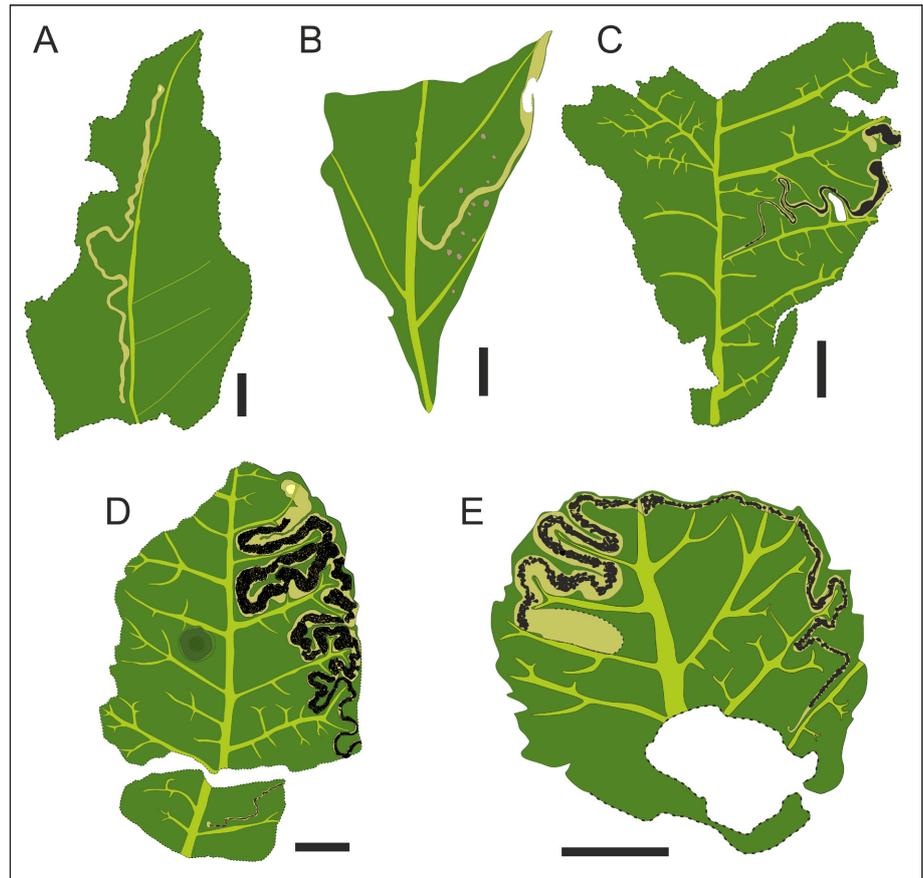
Cuniculonomus parallelus Givulescu, 1984

Fig. 2A; Fig. 3A

1982 Ophionome - Müller, p. 19, pl. 8, fig. 4

Syntypes: Specimens 1164, 1656 and 1807 B.J.B.M. on leaves of *Quercus* sp. (Fagaceae) or *Betula* sp. (Betulaceae) deposited in the collections of the Institute of Geology and Geophysics, Bucharest, Chiuzbaia Locality, Romania. Early Pliocene.
Emended diagnosis: Linear mines parallel to the middle leaf-host vein for most of its trajectory, which cross several secondary veins. These mines are completely developed on one half-leaf area.

Remarks. The diagnosis is emended here to include other characters that were absent in the original diagnosis of Givulescu (1984) and are typical of these leaf mines. The position on the leaf lamina and the trajectory of the leaf mine galleries cross several secondary veins. Givulescu (1984) focused the diagnosis on the reaction tissue and defined two possible preservational forms, forma alba and forma nigra, based on the coloration of the tissue. *Cuniculonomus parallelus* is different from *Cuniculonomus carpini* in having a partial of the mine paralleling the primary vein. The leaf mine described by Müller (1982) as "Ophionome" is considered here a synonym of *C. parallelus*.

Description. Slightly sinuous linear mines, from 2.9 cm to 8.6 cm length and from 0.1 mm to 0.26 mm in width. Mines occur parallel to the middle leaf-host throughout most of its extension and never intersect it. Mines originate near the basis of the leaf, ending at the apex or toward the leaf edge. Coprolites and terminal chamber are not discernable, although there is an exit hole with an oval shape (0.1 to 0.24 mm).

Host plants. Specimens CTES-IC 82 - *Nectandra saltensis* Anzótegui (Lauraceae); CTES-IC 54 - *Cedrela fissiliformis* Anzótegui & Horn (Meliaceae).

Cuniculonomus saltensis n. ichnosp.

Fig. 2B, C; Fig. 3B

1969 Larval leaf mining - Lewis, p. 1210

Derivatio nominis: *Saltensis* derives from Salta Province in northwestern Argentina where the fossil material crops out.
Holotype: Specimen CTES-IC 234a, on a leaf of *Cedrela fissiliformis*, collection from Facultad de Ciencias Exactas y Naturales y Agrimensura of the Universidad Nacional del Nordeste. Peñas Blancas locality, Salta, Argentina. Late Miocene.
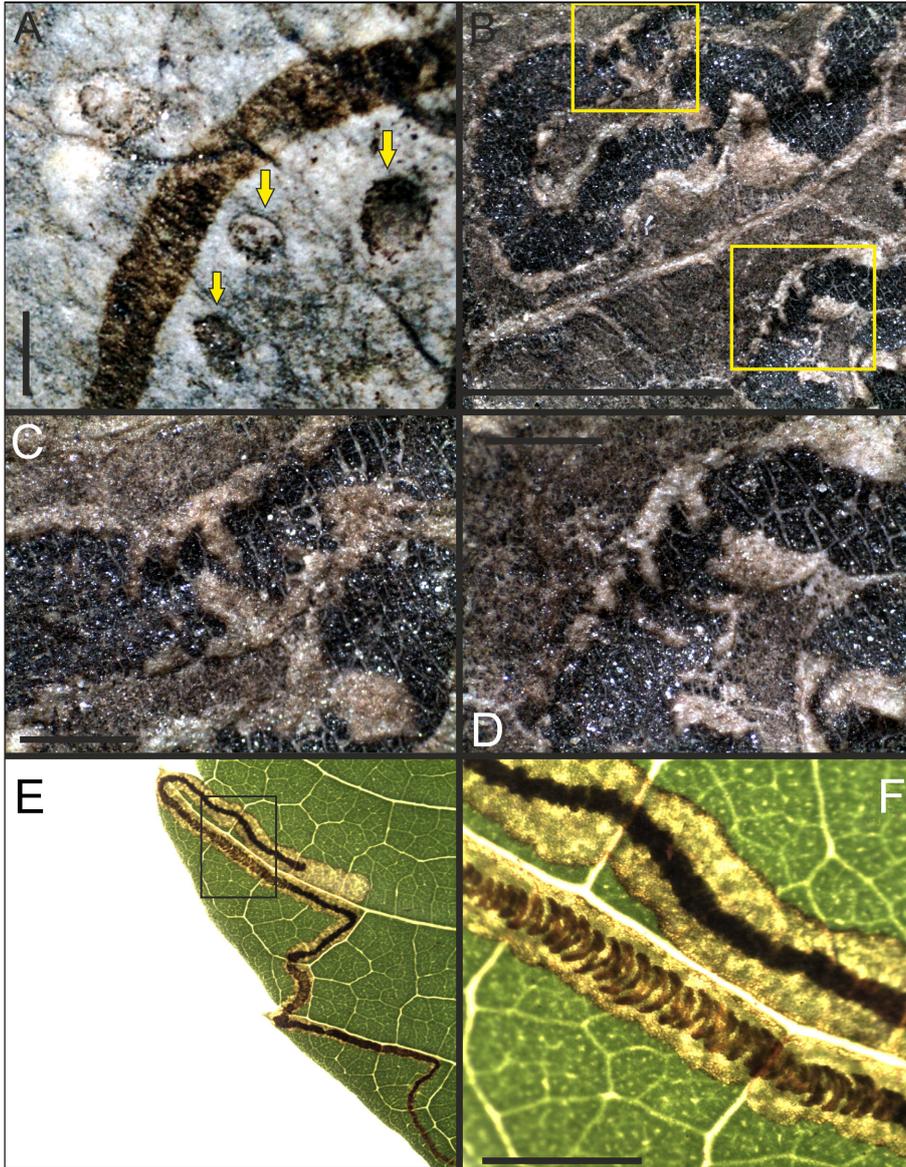
Fig. 4 - A) circular structures associated with the fossil mine (*Cuniculonomus saltensis* n. ichnosp.), possibly parasitoid-related features; B) in the sample CTES-IC 132 (*Stigmellites vitatus* n. ichnosp.), the fecal pellets are arranged in a zig-zag pattern; C and D) details of B; E) extant sample of the lepidopterous leaf mine; F) detail of E, showing the frass deposited in a zig-zag pattern, as in the fossil sample (CTES-IC 132). Bar scale= 0.5 mm (A, C, D and F); =3 mm (B).

Diagnosis: Linear mines located entirely between two primary or two secondary veins. Mines present with few interruptions and a slightly widening in the terminal segment is observed.

Depository: The material is deposited at the Paleontology Collection, Universidad Nacional del Nordeste.

Description. Specimens CTES-IC 234a and CTES-IC 152a, consist of partially conserved linear mines, with length varying from 22.55 mm to 31.12 mm and width from 0.25 mm to 0.75 mm. The origin of the mine is located adjacent to the primary vein or in a central region of the half-leaf between the midvein and margin subsequently coursing towards the margin and always remaining between two secondary veins. The mines present a widening at the terminal portion, which can triple the original mine width. There is no evidence of particulate coprolites.

Remarks. The complete leaf-mine ontogeny is developed between two adjacent secondary veins. The mine described by Lewis (1969) as "Lepidopterous larval-mining", is included here since the material documented by that author presents all the characters mentioned for *C. saltensis*. Lang et al. (1995) described a morphological type of mines (Type 2B), that correspond with mines that are entirely enclosed between two secondary veins; in all the specimens coprolites are observed and occasionally the terminal chamber is also preserved (V.50731, V.50089, V.48524, Mine 2, V.49808, V.50698, V.50622, V.50401). *Cuniculonomus saltensis* differs from the morphotype described by Lang et al. (1995) because coprolites and terminal chambers are absent. Donovan et al. (2014) reported fossil leaf mines located between two secondary veins that

present the same characteristics of those observed by Lang et al. (1995). In those specimens (Donovan et al. 2014), there is evidence for coprolites and/ or a terminal chamber (USNM 560118, USNM 560119, UNSM 561020). Specimens CTES-IC 236a and CTES-IC 152a were associated with galleries in which circular structures were found from 0.3 to 0.6 mm of diameter, similar to those described by Winkler et al. (2010), as agromyzid ovipositor marks (Fig. 4A).

Host plant. Specimens CTES-IC 152a and CTES-IC 234a, *Cedrela fissiliformis* Anzótegui & Horn (Meliaceae).

Ichnogenus *Stigmellites* Kernbach, 1967
Type ichnospecies: *S. heringi* (Kernbach, 1967)

Emended diagnosis: Linear mines located on one or both sides of the middle vein. These mines are located between two primary and/or secondary veins or alternatively passing through some veins. Mines end in a terminal chamber. Granular or threadlike coprolites are present in the central region of the mines.

Remarks. The diagnosis is emended here because of the unique character used by Kernbach (1967) to differentiate this ichnogenus from the possibility that the leaf miners are the larvae of the nepticulid lepidoteran *Stigmella*. The same author questioned the identification of the potential producers providing a reason for defining the ichnogenus *Stigmellites*.

Stigmellites serpentina Kozlov, 1988
Fig. 2F, G; Fig. 3C

1992 V.48524 - Stephenson & Scott, p. 549, fig. 6e.
1992 V.49808 - Stephenson & Scott, p. 548, fig. 5b.
1992 V.49808 - Scott et al., figs. 5a, b.
1995 V.48524 - Lang et al., p. 166, pl. 3 fig. 4.
1995 Mines type 2B V.50089 - Lang et al., p. 166 pl. 3 fig. 5.
1995 Mines type 2B Mine 2 - Lang et al., p. 163, pl. 2 fig. 2.
1995 V.49808 - Lang et al., p. 166, pl. 3 fig. 6.

Holotype: Specimen PIN, 2383/205, Beleu-Tinskaya Formation, Turonian (Upper Cretaceous), Kazakhstan.
Emended diagnosis: Serpentine mines completely enclosed between two primary or secondary veins. Coprolites are threadlike and mostly continuous forming an internal lineation within the gallery. Terminal chamber free of coprolites.

Description. The specimen CTES-IC 216 corresponds to a partially preserved serpentine mine in *Schinus herbstii*. The leaf-mine length is 32.15 mm and width from 0.10 mm to 0.44 mm. Terminal chamber is rectangular with length of 0.7 mm and width 0.5 mm. The mine originates near the midvein, at the junction with a secondary vein. It egresses sinuously to the margin without passing through the area between the two adjacent veins. The leaf mine gradually widens and ends near the margin of the leaf. Coprolites are located in center of the mine along almost all of the gallery length, except in the initial portion (length of the initial portion = 0.30 mm). Reaction tissue is poorly developed.

Remarks. The diagnosis is emended here to include the leaf area where the mine is located, which is not described by the author in the original description. In the holotype photo (Fig. 2F), it is clearly observed that the mine is located between two primary veins. Other specimens recorded by Lang et al. (1995) exhibit character similars to *S. serpentina,* although some mines pass through a secondary vein (V.50731 V.50698 V.50622 V. 50401) or a terminal chamber is not observed (V.49905). Samples USNM 560118, USNM 560119, UNSM 561020, USNM 56142 and USNM 56143 (Donovan et al. 2014, figs. 2A, E and D and figs. 8A and E), are situated between two secondary veins and have ellipsoidal pellets. These characters do not occur in *S. serpentina*, as the consistency of frass in one mine seems to be fluidized.

Host plant. *Schinus herbstii* Anzótegui (Anacardiaceae).

Stigmellites vitatus n. ichnosp.
Fig. 2D, E; Fig. 3 D

Derivatio nominis: From the Latin *Vito –atus*, meaning "shunning" or "avoidance".
Holotype: Specimen CTES-IC 132 occurs on a leaf of *Schinus herbstii*, deposited at the collection of the Facultad de Ciencias Exactas y Naturales y Agrimensura of the Universidad Nacional del Nordeste. Peñas Blancas locality, Salta, Argentina. The specimen is Late Miocene in age.
Diagnosis: Serpentine mines completely developed in one half-leaf area, originating at the leaf basis, either along the margin or near the midvein and extending toward the apex. Mines follow the margin of the leaf or course to the center of the leaf. Mines do not pass through the secondary veins or only do it in the apical region. Coprolites form a single continuous line and are present along the entire mine trajectory, except at the terminal mine phase. Mines end in a rectangular terminal chamber.
Depository: The material is deposited at the Paleontology Collection, Universidad Nacional del Nordeste.

Description. Specimen CTES-IC 132, is a serpentine mine (visceronoma type), length of 66.8 mm and width from 0.2 mm to 1.3 mm; the terminal chamber shows a rectangular outline, with length of 2.66 mm and width of 1.23 mm; the exit hole is circular and is placed in sub-terminal position in the terminal chamber, with diameter of 0.6 mm. This leaf mine starts adjacent the primary vein and subsequently approaches the foliar margin, gradually widening while it extends between secondary veins toward the central vein. The mine terminates near the leaf apex and it is only in this portion of the leaf where the trajectory crosses a secondary vein, which remains inside the mined area. Associated coprolites have a solid appearance, forming a single threadlike medial trail that occupies the center of the gallery with some sections seemingly deposited in zig-zag pattern (Fig. 4D-F). Frass is present throughout the mine trajectory, except in the final segment that corresponds to the terminal chamber. The reaction tissue is poorly developed, but it is possible to differentiate the mine within the leaf by the clearer hue of the gallery, that contrasts to the hue of the surrounding unaffected leaf tissue.

Remarks. *Stigmellites araliae* (Fritsch, 1882)*, S. fossilis* (von Heyden, 1862), *S. carpiniorientalis* (Straus, 1977), *S. zelkovae* (Straus, 1977), *S.* sp. (Kuroko, 1987); *S. kzyldzharica* (Kozlov, 1988) and *S. tyshchenkoi* (Kozlov, 1988) cross the middle or secondary veins. *Stigmellites vitatus* differs from these ichnospecies because is located entirely in one half leaf and never pass through the secondary veins, except in the apical region. Contrasting to *S. vitatus*, the frass preserved in *S. centennis* (Jarzembowski, 1989) is not medially positioned and the leaf mine is confined between two secondary veins. By contrast, *S. gossi* (Jarzembowski, 1989) has granular pelletal coprolites. *Stigmellites serpentina*, is the ichnospecies that shares more characters with *S. vitatus*, although the former is enclosed between two adjacent secondary veins. *Stigmellites samsonovi* and *S. sharovi* are different from *S. vitatus* because of their circular terminal chamber. Specimens V.50733 (Mine type 2A) and V.50731 (Mine type 2B) described by Scott, (1991), Stephenson & Scott (1992) and Lang et al. (1995), share some characters with *S. vitatus* with regard to the origin of the mine, the pattern and distribution of frass and the shape of the terminal chamber. Nevertheless, these mines are different from *S. vitatus* because the leaf mine in

those instances cross one or more secondary veins (V.50733, V.50731), lack apparent widening of the mine, except near the terminal chamber (V.50731), and display high sinuously along the mine's trajectory (V.50733).

Host plant. *Schinus herbstii* Anzótegui (Anacardiaceae).

Stigmellites pervenae n. ichnosp.
Fig. 2H; Fig. 3E

Derivatio nominis: From Latin *per* meaning "through" and *venae* meaning "veins".

Syntype: Specimens CTE-IC 169, CTE-IC 280a and CTES-IC 285a, on *Schinus herbstii*, deposited in the fossil collection of the Facultad de Ciencias Exactas y Naturales y Agrimensura of Universidad Nacional del Nordeste. Peñas Blancas locality, Salta, Argentina. Late Miocene.

Diagnosis: Serpentine mines developed on both sides of the primary vein. The mines originate in one half-leaf hemilamina, crossing the midvein once from left to right and back, ending on the opposite half leaf. The mines generally originate near the leaf apex, along the margin and close to the primary vein. During their path, the mines pass through the secondary veins and more finely-ranked veins. Threadlike coprolites formed into a single, medial file that course through almost all galleries. The mines end in a rectangular terminal chamber.

Depository: The material is deposited at the Paleontology Collection, Universidad Nacional del Nordeste.

Description. Specimen CTES-IC 43a is a serpentine mine (visceronoma type) with length of 40.30 mm and width from 0.13 mm to 1.62 mm; terminal chamber observed in sample CTES-IC 48a presents a rectangular outline with length 2.92 mm and width 1.33 mm; the exit hole is rounded and sub-terminal with a width of 0.64 mm of diameter. Mines originate close to the midvein (CTES-IC 43a) or on the foliar margin (CTES-IC 42, CTES-IC 169) and they cross all vein ranks, including the primary vein, which usually passes through in the apical region (CTES-IC 42, CTES-IC 48a and CTES-IC 169). Although the mines can also cross the primary vein in the central portion of the leaf (CTES-IC 43a) they also can culminate on the other half leaf side, either along the margin (CTES-IC 169) or adjacent to the midvein (CTES-IC 42, CTES-IC 43a and CTES-IC 48a). Coprolites are threadlike, lacking differentiation of fecal pellets, and occurring in center of the mine, where it occupies from 1/3 to almost the entire width of the mine. Coprolites are present throughout the entire mine, except in the terminal chamber. Reaction tissue is not clearly de-

veloped, but it is possible to differentiate the leaf mines from the unaffected leaf by the clearer hue of the mined region, compared to the more intense hues of the foliar blade.

Remarks. *Stigmellites pervenae* n. ichnosp. is distinctive because it is located at both sides of the midvein, and consequently on both half-leafs. *Stigmellites araliae, S. fossilis, S. carpiniorientalis,* and *S. zelkovae,* cross the secondary veins but not through primary veins. The mines in *S. centennis* and *S. serpentina* are enclosed between two secondary veins. By contrast, *S. gossi* presents coprolites that are differentiated in pellets and the mines are restricted to a third and/or fourth-ranked veins. Although *S. kzyldzharica* and *S. tyshchenkoi* are leaf mines crossing a middle vein, they are different from *S. pervenae* because the terminal chamber is absent and there is not a marked widening of the mine segments. Specimens V.50175, V.50744 and V.50719 (mines type 2A), recorded by Lang et al. (1995), show similar characteristics to *S. pervenae*. Specimen V.50719 displays a terminal chamber crossing the middle vein, but there is no evidence of coprolites in the mined area. The same characters are present in the specimen V.50744, occurring in the last-mentioned specimen, as the mine passes the middle vein twice. Thus, both the origin site and terminal chamber are located in the same half-leaf. V.50175 possibly corresponds to the same ichnospecies, but the terminal chamber is absent. Donovan et al. (2014) reported a serpentine mine crossing both half-leafs, but similarly the terminal chamber was not observed in this sample (DMNH 7511).

Host plant. *Schinus herbstii* Anzótegui (Anacardiaceae).

DISCUSSION

Perhaps attributable to their morphological distinctiveness the ichnotaxonomy of fossil leaf mines is highly developed compared with other insect-plant associations. Based on the specific morphology of certain leaf mines, some authors have named ichnogenera to refer to a particular possible producer. Some examples are the ichnogenera *Neptícula* (von Heyden 1862; Martins-Neto 1989), *Tinea* (Fritsch 1882), *Stigmella* (Kernbach 1967), *Phytomyza* (Hering 1930). However, Kelly (1990) and Bertling et al. (2006) suggested that

the definition of the ichnotaxon should not infer a particular tracemaker. To name an ichnotaxon based on a possible insect producer is incorrect, since several groups of insect leaf miner cause mines that share many morphological characters moreover these characters are not stables through the time (Winkler et al. 2010; Jud & Sohn 2016).

Several examples for this misuse can be cited from the fossil record. One example is the study of von Heyden (1862) who defined the ichnospecies *Neptícula fossilis* in a dicotyledonous host from the late Oligocene from Germany. However, Opler (1973) later reassigned the producer of this mine to a dipteran, arguing that the characters described by von Heyden were not diagnostic. For more examples, see Winkler et al. 2010. This is a reason why several authors such as Lang et al. (1995) suggested that the assignation of the producer insect should be based only at familial level or even at ordinal level. For instance, Winkler et al. (2010) proposed to expand the concept of *Phytomyzites* to include all those leaf mines produced by the Agromyzidae (Diptera). Bromley and Fürsich (1980; see also Kelly 1990; Stephenson 1991; Lang et al. 1995; Pemberton & McEachern 2013) outlined six of the fundamental principles of ichnology; one of which states that the nomenclature of fossil traces should be based only upon the morphological characters of the documented structure. Based on this construction and consideration of the proposals by Kelly (1990) and Bertling et al. (2006), and the nomenclature here proposed, should be established on the morphological characters commonly used in the analyzing of fossil mines (Lang et al. 1995; Crane & Jarzembowski 1980; Stephenson 1991).

The exceptions to the above caution of Kelly (1990) and Bertling et al. (2006) represent the ichnogenera *Stigmellites* and *Phytomyzites*, which were preserved here to maintain the nomenclatural stability. Several authors have considered the morphological characters of the leaf mine in order to define an ichnotaxon, e.g. *Cuniculonomus* defined by Straus (1977) on *Carpinus betulus* from the Pliocene of Germany. Later, Müller (1982) established four ichnospecies of *Cuniculonomus* on gymnosperm leaves from the Carboniferous and Permian of Germany, although these mines are not entirely convincing (Lang et al. 1995). Gi-

Characters	*Cuniculonomus*	*Stigmellites*	*Phytomyzites*
1) Oviposition area	Larger lenticular lesion (oviposition mark); surrounded or not by several smaller ovipositional probes	Larger lenticular lesions; surrounding ovipositions probes absent.	Single, small lenticular lesion, surrounded by several smaller ovipositional probes.
2) Widening of the mine (except the terminal chamber)	It can widen up to 3 times.	It can widen up to 12 times.	It can widen up to 4 times.
3) Coprolites shape and disposition	Not observable	Differentiated or not in faecal pellets; mainly continuous it can be cut only where the mines cross the leaf veins; located in center of the leaf-mine.	Not differentiated (fluid consistence); intermittent in at least one part of the mine; located in center of the leaf-mine, but in some segments, the frass can alternate in both sides of internal margins of the leaf mine
4) Sinuosity of the mine	Slightly sinuous. No more of 1 or 2 deviations of 180º	Highly sinuous (serpentines); > 2 deviations of 180º; The traces never overlap a section previously formed.	From slight to highly sinuous (serpentines), from 1 to several deviations of 180º. They can overlap a section previously formed
5) Terminal/Pupal chamber	Absent	Present, variously shaped.	Present, variously shaped.

Tab. 1 - The table shows the characters used to differentiate the ichnogenera *Cuniculonomus*, *Stigmellites* and *Phytomyzites*.

vulescu (1984) described *Cuniculonomus parallelus* on *Quercus* sp. an oak from the late Miocene of Romania. Rozefelds & Sobbe (1987) defined the ichnospecies *Triassohyponomus dimnoriensis* consisting of linear mines on leaves of the voltzialean conifer *Heidiphyllum elongatum* from the late Triassic of Australia. Finally, Jarzembowski (1989) defined the ichnospecies *Foliofossor cranei* on *Platanus schimperi* a sycamore from the late Paleocene of England. In accordance with the suggestions of Kelly (1990) and Bertling et al. (2006), we emended herein, the diagnosis of *Cuniculonomus* and *Stigmellites*, and the ichnospecies analyzed in this work *Cuniculonomus parallelus* and *Stigmellites serpentina*, to include leaf-mine morphological characters useful for comparison with other ichnotaxa.

Hering (1951) proposed a classification based on the morphological character of extant leaf mines. Using Hering's classification, Krassilov (2008a) described eleven leaf-mine fossil ichnogenera with 28 ichnospecies on leaves of basal angiosperms from the Late Cretaceous of Israel. Of the ichnospecies recorded, eleven correspond with linear mines or a combination of linear and blotch mines. Two of these ichnospecies should be synonymous of the ichnogenus *Phytomyzites*. The ichnospecies *Ophionoma arcuata* displays discontinuous coprolites in the center of the gallery and a slightly widening terminus, possibly indicate a terminal or pupation chamber. In *Troponoma crucitracta* there is overlapping of the leaf mine, a slight sinuosity in the mine trajectory and intermittent coprolites that are sometimes deposited in double row. The changes described above are attributable to *Ophionoma arcuata* and *Troponoma crucitracta* exhibiting diagnosis coincident with *Phytomyzites*.

To achieve a nomenclatural clarity a series of characters (ichnotaxobases) is proposed to differentiate the ichnogenera *Stigmellites*, *Cuniculonomus* and *Phytomyzites* (Tab. 1). These ichnotaxobases, proposed only for mines do not apply to other type of plant-insect association. These ichnotaxobases are restricted to linear to tightly sinusoidal mines, exclude blotch mines, and are relatively easy to recognize in fossil leaves and present two or more variants (detailed in the introduction section) that allow clear differentiation of the ichnogenera. In terms of behavior, these characters also provide significant information, such as the presence of terminal chamber that inevitably reflects a completed mine, where the larva frequently reached its pre-pupal stage. Likewise, the sinuosity of mine is often associated with the venational meshwork of leaves, as larvae are commonly unable to pass through higher ranked veins, especially in early stages, causing highly sinuous mines (Hering 1951). These leaf-mine characters listed above also are relevant in studies focusing on the identification of insect leaf miners. For example, Winkler et al. (2010) showed that the consistency and disposition of coprolites, as well as the sinuosity of mines and features such as overlapping trajectories are reliable characteristics to identify agromyzid mines

(Diptera). Similarly, Doorenweerd et al. (2015) detailed a listed of morphological characters to identify fossil mines produced by nepticulids, which they included data about shape of mines, the terminal chamber and coprolites. As a result of these developments, this contribution is the first attempt to unify the ichnotaxonomy of linear mines, focusing particularly on the morphology and establishing ichnotaxobases that would provide valuable information about the producer insect and its feeding behavior and thereby increasing knowledge of the leaf-miner fauna in the Neogene flora from Argentina.

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APPENDIX

Ichnotaxa	Formation/Age /Country	Host plant	Possible insect producer	Reference	Synonymy
Cuniculonomus carpini Straus	Formation?, Late Pliocene, Germany	*Carpinus betulus* (Betulaceae)	Agromyzidae? (Diptera)	Straus 1977	
Phytomyzites corni Straus	Formation?, Late Pliocene, Germany	*Cornus* sp.? (Cornaceae)	Agromyzidae	Straus 1977	
Stigmellites carpiniorientalis Straus	Formation?, Late Pliocene, Germany	*Carpinus orientalis* (Betulaceae)	Nepticulidae (Lepidoptera)	Sohn et al. 2012	*S. carpini-orientalis* Straus 1977
Stigmellites heringi Kernbach	Formation?, Late Pliocene, Germany	*Berberis* sp. (Berberidaceae)	Nepticulidae	Kernbach 1967	
Stigmellites pliotityrella Kernbach	Formation? Late Pliocene, Germany	*Fagus* sp. (Fagaceae)	Nepticulidae	Doorenweerd et al. 2015	*Stigmella pliotityrella* (Kernbach 1967); *Stigmellites pliotityrellus* Sohn et al. 2012
Stigmellites zelkovae Straus	Formation?, Late Pliocene, Germany	*Zelkova* sp. (Ulmaceae)	Nepticulidae	Straus 1977	
Cuniculonomus parallelus Givulescu	Formation?, Late Miocene, Romania	*Quercus* sp. (Fagaceae)	Agromyzidae?	Givulescu 1984	
Cuniculonomus saltensis nov. ichnosp.	Palo Pintado Formation, Late Miocene, Argentina	*Cedrela fissiliformis* (Meliaceae)	Gracillariidae? (Lepidoptera)	This paper	
Phytomyzites lethe Hering	Formation?, Late Miocene, Germany	?	Agromyzidae	This paper	Comb nov. from *Phytomyza lethe* Hering 1930
Phytomyzites querci Givulescu	Formation?, Late Miocene, Romania	*Quercus* sp. (Fagaceae)	Agromyzidae	Givulescu 1984	
Stigmellites pervenae nov. ichnosp.	Palo Pintado Formation, Late Miocene, Argentina	*Schinus herbstii* (Anacardiaceae)	Nepticulidae?	This paper	
Stigmellites vitatus nov. ichnosp.	Palo Pintado Formation, Late Miocene, Argentina	*Schinus herbstii* (Anacardiaceae)	Nepticulidae?	This paper	
Stigmellites sp.	Formation?, Late Miocene, Japan	*Betula grossa* (Betulaceae)	Nepticulidae	This paper	*Stigmella* sp.
Stigmellites almeidae Martins-Neto	Tremembé Formation, Oligocene, Brazil	cf. *Symplocos* sp. (Symplocaceae)	Nepticulidae	Doorenweerd et al. 2015	*Nepticula*? *almeidae* Martins-Neto 1989
Stigmellites fossilis Von Heyden	Rott Formation, Late Oligocene, Germany	*Juglans acuminate* (Juglandaceae)	Nepticulidae	Kozlov 1988	*Nepticula fossilis* Von Heyden 1862
Phytomyzites schaarschmidti Wappler	Messel Formation, Middle Eocene, Germany	*Toddalia ovata* (Rutaceae)	Agromyzidae	Winkler et al. 2010	
Stigmellites messelensis Straus	Messel Formation, Middle Eocene, Germany	?	Nepticulidae	Straus 1976	

Ichnospecies of linear mines known in the fossil record. (continue)

Ichnospecies of linear mines known in the fossil record. (continue)

Ichnotaxa	Formation/Age /Country	Host plant	Possible insect producer	Reference	Synonymy
Foliofossor cranei Jarzemwoski	Reading Formation, Late Paleocene, England	*Platanus Schimperi* (Platanaceae)	Agromyzidae?	Jarzembowski 1989	
Stigmellites centennis Jarzembowski	Reading Formation, Late Paleocene, England	Fabaceae?	Nepticulidae	Sohn et al. 2012	*Stigmellites? centennis* Jarzembowski, 1989
Stigmellites gossi Jarzembowski	Reading Formation, Late Paleocene, England	dicotyledon	Nepticulidae	Sohn et al. 2012	*Stigmellites? gossi* Jarzembowski 1989
Phytomyzites biliapchaensis Winkler, Labandeira & Wilf	Fort Union Formation, Early Paleocene, USA	*Platanus Raynoldsii* (Platanaceae)	Agromyzidae	Winkler et al. 2009	
Stigmellites araliae Fristch	Perucher Formation, Late Cretaceous, Czech Republic	*Aralia* sp. (Araliaceae)	Nepticulidae	Kozlov 1988	*Tinea araliae* Fristch 1882
Stigmellites kzyldzharica Kozlov	Beleuty Formation, Late Cretaceous, Kazakhstan	*Platanus ambicula* (Platanaceae)	Nepticulidae	Doorenweerd et al. 2015	*Stigmellites kzyldzharicus* Sohn et al. 2012
Stigmellites samsonovi Kozlov	*Beleuty Formation, Late Cretaceous, Kazakhstan*	*Trochodendroides arctica* (Cercidiphyllaceae)	Nepticulidae	Kozlov 1988	
Stigmellites serpentina Kozlov	*Beleuty Formation, Late Cretaceous, Kazakhstan*	*Trochodendroides arctica* (Cercidiphyllaceae)	Nepticulidae	Kozlov 1988	
Stigmellites sharovi Kozlov	*Beleuty Formation, Late Cretaceous, Kazakhstan*	*Trochodendroides arctica* (Cercidiphyllaceae)	Nepticulidae	Kozlov 1988	
Stigmellites tyshchenkoi Kozlov	*Beleuty Formation, Late Cretaceous, Kazakhstan*	*Platanus latior* (Platanaceae)	Nepticulidae	Kozlov 1988	
Ophionoma digitata Krassilov	Upper Hatira and Ora Formations, Middle Cretaceous, Israel	*Dewalquea gerofitica* (family incertae sedis); *Eocercidiphyllites glandulosus* (Cercidiphyllaceae)	Gracillariidae	Krassilov 2008a	
Ophionoma paradroma Krassilov	Upper Hatira and Ora Formations, Middle Cretaceous, Israel	*Typhacites negevensis* (Typhaceae?)	Noctuidae (Lepidoptera), Agromyzidae	Krassilov 2008a	
Ophionoma serranoides Krassilov	Upper Hatira and Ora Formations, Middle Cretaceous, Israel	*Platydebeya papilionácea* (family incertae sedis); *Nelumbites aravensis* (Nelumbonaceae)	Tenthredinidae (Hymenoptera)	Krassilov 2008a	

Ichnotaxa	Formation/Age /Country	Host plant	Possible insect producer	Reference	Synonymy
Ophistigmonoma crassa Krassilov	Upper Hatira and Ora Formations, Middle Cretaceous, Israel	*Eudebeya angusta* (family incertae sedis)*; Platydebeya papilionácea* (Papilionaceae)*; Nelumbites aravensis* (Nelumbonaceae); *Eocercidiphyllites glandulosus* (Cercidiphyllaceae)	Bucculatricidae (Lepidoptera)	Krassilov 2008a	
Ophistigmonoma rectiserialis Krassilov	Upper Hatira and Ora Formations, Middle Cretaceous, Israel	*Dewalquea gerofitica* (family incertae sedis)	Diptera	Krassilov 2008a	
Phytomyzites arcuata Krassilov	Upper Hatira and Ora Formations, Middle Cretaceous, Israel	*Dewalquea gerofitica* (family incertae sedis)	Agromyzidae	This paper	Comb. nov. from *Ophionoma* Krassilov 2008a
Phytomyzites crucitracta Krassilov	Upper Hatira and Ora Formations, Middle Cretaceous, Israel	*Platanervia integrifolia* (Platanaceae)	Gracilariidae, Gelechiidae (Lepidoptera), Agromyzidae	This paper	Comb. nov. from *Troponoma* Krassilov 2008a
Stigmellites resupinata Krassilov	Upper Hatira and Ora Formations, Middle Cretaceous, Israel	*Dewalquea gerofitica* (family incertae sedis)	Nepticulidae	Doorenweerd et al. 2015	*Ophiheliconoma resupinata* Krassilov 2008a
Troponoma constricta Krassilov & Bacchia	Akrabou Formation, Middle Cretaceous, Morroco	*Cocculophyllum* cf. *furcinerve* (Lauraceae?)	?	Krassilov & Bacchia 2012	
Fossafolia offae Ding, Labandeira & Ren	Yixian Formation, Early Cretaceous, China	*Liaoningocladus boii* (family incertae sedis)	Buprestidae (Coleoptera)	Ding et al. 2014	
Phytomyzites wardi Jud & Sohn	Patapsco Formation, Lower Cretaceous, USA	*Vernifolium tenuiloba* (family incertae sedis)	Agromyzidae	Jud & Sohn 2016	
Triassohyponomus dinmorensis Rozefelds & Sobbe	Blackstone Formation, Late Triassic, Australia	*Heidiphyllum elongatum* (Voltziaceae)	?	Rozefelds & Sobbe 1987	
Cuniculonomus tenuis Müller	Formation?, Permian?, Germany	*Odontoperis lingulata* (Schizaeaceae)	Agromyzidae	Müller 1982	
Asteronomus meandriformis Müller	Formation?, Lower Permian, Germany	*Autunia conferta* (Peltaspermaceae)	?	Müller 1982	
Cuniculonomus subtilis Müller	Formation?, Late Carboniferous, Germany	*Neuropteris britannica* (Neuropteridaceae)	Nepticulidae	Müller 1982	

Ichnospecies of linear mines known in the fossil record.