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DISTINGUISHING AGROMYZIDAE (DIPTERA) LEAF MINES IN THE FOSSIL RECORD: NEW TAXA FROM THE PALEOGENE OF NORTH AMERICA AND GERMANY AND THEIR EVOLUTIONARY IMPLICATIONS

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ABSTRACT—Fossilized leaf mines and other traces of phytophagous insects provide a unique window into ecological and evolutionary associations of the past. Leaf-mining flies (Diptera: Agromyzidae) are an important component of the recent leaf-mining fauna, but their fossil record is sparse compared to other mining insect lineages; many putative agromyzid body fossils and traces are dubiously assigned. Agromyzid leaf mines often can be distinguished from those of other insects by the presence of an intermittent, fluidized frass trail that may alternate between the sides of the mine. Here, we describe two new Paleogene leaf mine fossils, *Phytomyzites biliapchaensis* Winkler, Labandeira and Wilf **n. sp.** from the early Paleocene of southeastern Montana, USA, occurring in leaves of *Platanus raynoldsii* (Platanaceae); and *Phytomyzites schaarschmidti* Wappler **n. sp.**, from the middle Eocene of Messel, Germany, occurring in leaves of *Toddalia ovata* (Rutaceae). These fossils both exhibit frass trails indicative of an agromyzid origin, and *P. biliapchaensis* also exhibits associated stereotypical marks identical to damage caused by feeding punctures of extant adult female Agromyzidae prior to oviposition. *Phytomyzites biliapchaensis* represents the earliest confirmed record of Agromyzidae, and one of the earliest records for the large dipteran clade Schizophora. Plant hosts of both species belong to genera that are no longer hosts of leaf-mining Agromyzidae, suggesting a complex and dynamic history of early host-plant associations and, for the early Paleocene example, an evolutionary, possibly opportunistic colonization in the midst of the ecological chaos following the end-Cretaceous event in North America.

INTRODUCTION

FOSSILIZED PLANT tissues containing distinctive insect-feeding damage represent important evidence for investigating the ecology and evolution of ancient ecosystems (Labandeira, 1998a, 2006; Wilf and Labandeira, 1999; Zherikhin, 2002). Leaf mines, the traces of insect larvae feeding internally on leaf tissues typically beneath the epidermis, are common, and they have been reported repeatedly as fossils (Straus, 1977; Crane and Jarzembowski, 1980; Lang et al., 1995; Labandeira, 2002; Krassilov, 2008a). In some cases, distinctive feeding patterns observed in fossil leaf mines closely match those of extant taxa, in which case the fossils have important implications for the evolution of specific insect groups (Opler, 1973; Labandeira et al., 1994, 1998b; Lopez-Vaamonde et al., 2006). However, taxonomic assignment of leaf mines can be problematic because insects from multiple orders and many families produce them, and mine morphology may not be phylogenetically stable through time (Grimaldi, 1999; Labandeira, 1998b, 2002a). Furthermore, many characteristics of leaf mines, including overall shape and pattern of frass deposition, often vary within taxonomic groups and even among closely related species (Hering, 1957; Spencer, 1990).

Sixteen families of Diptera (true flies) include leaf- and stem-mining species, but these mostly belong to small groups of miners in families with other predominant feeding habits (Labandeira, 2005). The exception is the family Agromyzidae (leaf-mining flies), a large, diverse (2,800 spp.), and abundant group of internally-feeding phytophagous insects feeding on a wide variety of angiospermous plants (Spencer, 1990), as well as on a few non-angiosperms. As indicated by the common

name, larvae of most agromyzid flies are leaf-miners, but the family includes some species that feed in stems, flower heads and seeds, roots, twig galls, and cambial or xylary tissues of arborescent plants.

The majority of extant agromyzid species are found on herbaceous plants, but at least 40 extant species in eight genera mine leaves of arborescent species (Spencer, 1990). It appears that leaf-mining on trees has evolved several times within the Agromyzidae, but this trait is not characterized by a high diversity of fly or host-plant species. In contrast, several families of leaf-mining Lepidoptera are abundant and diverse on a wide variety of tree hosts, and less often attack herbaceous plants (Connor and Taverner, 1997; Powell et al., 1998). Leaf mines of lepidopterous origin are much more common than dipteran traces in the fossil record. This may be largely attributable to the fact that leaves from large, persistent plants are much more likely to enter the fossil record. Additionally, leaf mining is an ancient and common mode of life among early, basal families of Lepidoptera (Labandeira et al., 1994; Powell et al., 1998). Because of this historical incumbency and preference for woody plant hosts, a wide variety of leaf mines probably attributable to Lepidoptera have been reported from the fossil record starting from the latest Early Cretaceous (Kozlov, 1988; Labandeira, 2006). Mines resembling those of the moth families Nepticulidae, a relatively ancient leaf-mining lineage, and Gracillariidae are especially abundant and diverse in the fossil record (Opler, 1973; Labandeira et al., 1994; Lang et al., 1995; Labandeira, 2002; Lopez-Vaamonde et al., 2006).

Leaf-mining in the order Coleoptera (beetles) is of more ancient origin; the earliest demonstrable leaf mine fossils—

from the Late Triassic of South Africa, Australia, and Kyrgyzstan (Rozeffelds, 1985; Rozeffelds and Sobbe, 1987; Zherikin, 2002; Scott et al., 2004)—may be attributable to this order (Labandeira and Anderson, 2005; Labandeira, 2006a, 2006b). Beetle traces often resemble closely those of Lepidoptera, due to the similar form of the larval mouthparts. However, leaf-mining Coleoptera represent a small proportion of extant leaf-mining taxa. Lastly, very rare mines attributable to symphytan Hymenoptera have been noted in Paleogene deposits (Wilf et al., 2006).

The fossil record of Agromyzidae is sparse and poorly studied (Table 1), and many fossils have probably been incorrectly referred to the family (Spencer and Martinez, 1987). Although putative agromyzid mines have been reported from the Paleocene (Crane and Jarzembowski, 1980), and even from the Late Cretaceous (Turonian; Krassilov, 2007, 2008a, 2008b), until recently the earliest confirmable evidence of agromyzid flies was from early middle Eocene borings in fossilized wood (Süss and Müller-Stoll, 1980). Wilf et al. (2006) reported agromyzid leaf mines from the early Paleocene of southeastern Montana, USA, and we consider these to be the oldest known record of Agromyzidae. These locally abundant fossils were briefly characterized and figured by Wilf et al. (2006), and more recently by Winkler et al. (2009b), who used them to calibrate a time scale of agromyzid evolution.

In this paper, we formally describe the Paleocene Montana leaf mines as a new ichnospecies attributed to Agromyzidae, and comment in detail on characters supporting this attribution. In addition, we describe another, somewhat more recent agromyzid mine from the early middle Eocene of Messel, Germany. These fossils represent important early occurrences of the large dipteran clade Schizophora (~27,000 spp.) and, added to previously described material, suggest an early Paleogene diversification of the major extant agromyzid lineages. The host plants in which these two fossil mines occur belong to genera (and one to a family) that are no longer hosts of extant agromyzid leaf miners, demonstrating a more complex and dynamic history of host associations than indicated by extant Agromyzidae alone. We clarify the fossil record of Agromyzidae by critically reviewing fossils previously attributed to Agromyzidae and commenting on distinctive characteristics of agromyzid mines that will allow more accurate identification of fossil material.

FOSSIL RECORD OF AGROMYZIDAE

Evenhuis (1994) lists 20 fossil names under Agromyzidae, including both body fossils and trace fossils (Table 1). The following review of these and other putative agromyzid fossils reveals that this assignment was, in many cases, based on superficial similarities, and should not be considered conclusive. Nonetheless, several described fossils are definitely attributable to Agromyzidae; these are discussed first below. Melander (1949) described three species from the Florissant fossil beds, recently referred to the latest Eocene (Evanoff et al., 2001), which may belong to extant genera. These Florissant fossils show exceptional preservation, such that even some details of the original coloration are clearly visible. For one of these, *Agromyza praecursor* Melander 1949, he noted a strong resemblance, especially in antennal characteristics (expanded third segment), to species now placed in the subgenus *Cerodontha* (*Dizygomyza*) Hendel, 1920. This suggests a relatively derived placement in the family (Scheffer et al., 2007), though an expanded antennal segment may have evolved independently in other lineages. Melander placed his

two other fossil species in *Melanagromyza* Hendel 1920 because of the visibly darkened haltere, a knob-like structure homologous to a reduced hind-wing in Diptera. This character is shared with several related genera now considered distinct from *Melanagromyza*, and the pale-colored legs of *M. tephrias* Melander, 1949, suggest that at least this species belongs to another genus. Zlobin (2007) revisited previously described material from the Isle of Wight (Bembridge Marls, late Eocene) and noted specimens attributable by wing characteristics to both extant subfamilies of Agromyzidae (Agromyzinae and Phytomyzinae). However, poor preservation did not allow generic assignment of these fossils.

Important evidence on the early evolution of Agromyzidae is provided by a class of traces known as “Markflecke” or “pith flecks.” These are formed by the agromyzid genus *Phytobia* Lioy, 1864, whose larvae bore in the cambium layer of trees, or just beneath in the layer of differentiating xylem cells, creating stereotypical patterns of damage in the wood as it matures (Fig. 1.1; Spencer, 1973; Solomon, 1995; Ylioja et al., 1998). Of extant *Phytobia*, host-plant identity is known only for a few temperate species, but the distinctive feeding damage has been noted in wood from a wide variety of temperate and tropical tree species (Süss and Müller-Stoll, 1980). Identical damage has been noted in fossil woods (Figs. 1.3–1.4), and several examples were described under the ichnogenera *Palaeophytobia* Süss and Müller-Stoll, 1975 and *Protophytobia* Süss, 1979 (Süss, 1979, 1980; Süss in Geissert et al., 1981; Süss and Müller-Stoll, 1975, 1977, 1980, 1982; see also Kräusel and Schönfeld, 1925; Grambast-Fessart, 1966; Süss and Velitzelos, 2001). The oldest known example of putative *Phytobia* traces, *Palaeophytobia prunorum* Süss and Müller-Stoll, 1980, is from the Amethyst Mountain locality in Yellowstone National Park, Wyoming, which has been dated at approximately 50 Ma (early middle Eocene; Smedes and Prostka, 1972). The only other insect group that is known to form similar cambium mines is the little-known moth family Opostegidae (Davis, 1989; Fig. 1.2). The single study directly comparing opostegid to *Phytobia* traces (Kumada, 1984) found that *Phytobia* mines do have distinctive features, including an elongate shape when viewed in cross-section, and mines of later instars can be easily distinguished from opostegid mines in the same host (Figs. 1.1–1.2). The description of *Palaeophytobia prunorum* (Süss and Müller-Stoll, 1980) notes this tangential elongation, as well as stereotypical secondary cellular growth in response to the feeding damage, strongly suggesting that this fossil in fact represents a typical *Phytobia* trace.

Because *Phytobia* species exhibit several presumably plesiomorphic characters, including large size, their feeding habits were once thought to represent the ancestral agromyzid condition (e.g., Nowakowski, 1962). However, recent phylogenetic work (Dempewolf, 2001; Scheffer et al., 2007) has shown that *Phytobia* is more derived within Agromyzidae than previously thought, and the leaf-mining habit is instead probably ancestral for the family. The host plant of the Eocene *Palaeophytobia prunorum* is *Pruninium* Platen, 1908, analogous to extant *Prunus* L. of the Rosaceae, which is shared by at least two extant species of *Phytobia*. Accordingly, it is possible, given the generally conservative nature of host-use evolution in this family, that this species could be relatively derived even within *Phytobia*. In any case, it appears that the origin of Agromyzidae may substantially predate *Palaeophytobia* fossils.

Additional fossils exist that have been more questionably assigned to Agromyzidae. Of the body fossils originally

TABLE 1—Synopsis of named fossils originally or later attributed to Agromyzidae. Sources: Evenhuis (1994), Spencer and Martinez, (1987), Labandeira (2005). For additional details consult these sources. Status: NA – not accepted as an agromyzid. U – uncertain or doubtful, A – Accepted as belonging to Agromyzidae.

Fossil	Deposit and fossil type	Locality/age	Host plant	Reference	Status	Notes
<i>Asteronema arachnoides</i> , <i>A. helicoides</i> , <i>A. expansa</i> Krassilov	Compression, (leaf mines?)	Israel [Cretaceous: Turonian]	<i>Nelumbites</i> (Nelumbonaceae), <i>Platydebeva</i> (Menispermaceae?)	Krassilov (2007, 2008a,b)	NA	Regular double rows of “frass pellets” not analogous to modern Agromyzidae; possibly oviposition or mandibular marks.
<i>Foliofossor cranei</i> Jarzembowski	Compression, (leaf mine)	UK [Paleocene]	unknown	Jarzembowski (1989), Crane and Jarzembowski (1980)	NA	No frass trail visible; considered by Kozlov (1988) as a nepticulid moth.
<i>Palaeophytobia prunorum</i> Süss & Müller-Stoll	Permineralization, (wood borings)	USA [Eocene]	<i>Pruninium</i> (Rosaceae)	Süss and Müller-Stoll (1980, 1982)	A	“Pith flecks” in wood, analogous to <i>Phytobia</i> traces.
<i>Agromyza praecursor</i> Melander	Compression, (body fossil)	USA [Eocene]		Melander (1949)	A	May belong to group (<i>Dizygomyza</i>) now included in genus <i>Cerodontha</i> .
<i>Melanagromyza prisca</i> Melander	Compression, (body fossil)	USA [Eocene]		Melander (1949)	A	Well-preserved; at least family placement certain.
<i>Melanagromyza tephrias</i> Melander	Compression, (body fossil)	USA [Eocene]		Melander (1949)	A	Well-preserved; at least family placement certain.
<i>Eomyza holoptera</i> Cockerell	Compression, (body fossil)	USA [Eocene]		Cockerell (1924), Hendel (1931–1936)	NA	Not an agromyzid in modern sense (Hendel, 1931–1936).
<i>Agromyza meunieri</i> Hendel	Amber, (body fossil)	Baltic Amber [Eocene]		Hennig (1965)	NA	Clusiidae; nom. nov. for <i>A. minuta</i> Meunier.
<i>Agromyza aberrans</i> Meunier	Amber, (body fossil)	Baltic amber [Eocene]		Hennig (1965), Hendel (1931–1936)	NA	“Possibly Chloropidae”
<i>Napomyza robusta</i> Meunier	Amber, (body fossil)	Baltic amber [Eocene]		Hennig (1965)	NA	Sciadoceridae (now included as a synonym in Phoridae).
“ <i>Phytoptus</i> ” <i>antiques</i> von Heyden	Compression, (leaf mine)	Germany [Oligocene]		von Heyden (1862), Sittig (1927)	U	Apparently identical to mine described by Berger (1949; see Table 2).
<i>Protonapomyza</i> Quiévreux	Compression, (body fossil)	France [Oligocene]		Quiévreux (1934, 1935)	U	Apparently never described nor assigned a type (listed only).
<i>Agromyza incerta</i> Théobald	Compression, (body fossil)	France [Oligocene]		Hennig (1965)	U	“Unidentifiable”
<i>Agromyza serresi</i> Théobald	Compression, (body fossil)	France [Oligocene]		Hennig (1965)	U	“Unidentifiable”
<i>Protophytobia cupressorum</i> Süss	Permineralization, (wood borings)	Netherlands [undetermined Paleogene]	<i>Juniperoxylon</i> (Cupressaceae)	Süss (1979), Kräusel and Schönfeld (1924)	A	“Pith flecks” in wood, analogous to <i>Phytobia</i> traces.
<i>Palaeophytobia platani</i> Süss & Müller-Stoll	Permineralization, (wood borings)	Hungary [Miocene]	<i>Platanoxylon</i> (Platanaceae)	Süss and Müller-Stoll (1975, 1977)	A	“Pith flecks” in wood, analogous to <i>Phytobia</i> traces.
<i>Agromyza protogaea</i> Heer	Compression, (body fossil)	Croatia [Miocene]		Hendel (1931–1936)	U	“Unidentifiable”
<i>Phytomyza lethe</i> Hering	Compression, (leaf mine)	Germany [Miocene]	Unknown	Hering (1930), Hendel (1931–1936)	U	Hendel (1931–1936) questioned assignment, but at least family placement possible.
<i>Palaeophytobia salicaria</i> Süss	Permineralization, (wood borings)	Germany [Pliocene]	<i>Populoxylon</i> (Salicaceae)	Geissert et al. (1981)	A	“Pith flecks” in wood, analogous to <i>Phytobia</i> traces.
<i>Phytagromyza populicola fossilis</i> Straus	Compression, (leaf mine)	Germany [Pliocene]	<i>Populus</i> (Salicaceae)	Straus (1977)	A	Possibly represents extant species <i>Aulagromyza populicola</i> or related species.
<i>Phytomyza ranunculi fossilis</i> Dürrenfeldt	Compression, (leaf mine)	Germany [Pliocene]	<i>Ranunculus</i> (Ranunculaceae)	Straus (1967, 1977)	A	Mine similar to extant <i>Phytomyza stolonigena</i> .

TABLE 1—Continued.

Fossil	Deposit and fossil type	Locality/age	Host plant	Reference	Status	Notes
<i>Phytomyzites corni</i> Straus	Compression, (leaf mine)	Germany [Pliocene]	<i>Cornus</i> (Cornaceae)	Straus (1977)	A	Possibly extant species <i>Phytomyza agromyzina</i> on same host.
<i>Cuniculonomus carpini</i> Straus	Compression, leaf mine	Germany [Pliocene]	<i>Carpinus</i> (Betulaceae)	Straus (1977), Evenhuis (1994)	U	Originally listed under “indefinite mines.”
<i>Cuniculonomus parallelus</i> Givulescu	Compression, (leaf mine)	Romania [Pliocene]	<i>Betula</i> (Betulaceae) or <i>Quercus</i> (Fagaceae)	Givulescu (1984)	U	Originally listed under “Mines of undeterminable Appurtenance.”
<i>Loconomus vitis</i> Straus	Compression, (leaf mine)	Germany [Pliocene]	<i>Vitis</i> (Vitaceae)	Straus (1977)	U	Originally listed under “indefinite mines.”
<i>Phytomyzites querci</i> Givulescu	Compression, (leaf mine)	Romania [Pliocene]	<i>Quercus</i> (Fagaceae)	Givulescu (1984)	U	No features suggestive of agromyzid origin given, host identity suggests lepidopteran origin.
<i>Phytomyza vetusta</i> Théobald	Compression, (body fossil)	Germany [Pliocene]		Hennig (1965)	U	“Unidentifiable.”

assigned to Agromyzidae, four fossils were later listed as “unidentifiable” by Hendel (1931–1936) and Hennig (1965), and one other (*Eomyza holoptera* Cockerell, 1924) was placed rather arbitrarily in Agromyzidae, but cannot be an agromyzid based on the modern concept of the family (Hendel, 1931–1936). Another fossil, from the early Oligocene of France, was listed as the genus *Protonapomyza* (Quiévreux, 1934, 1935); apparently, no descriptive information is available for this fossil. Hennig (1965) transferred all three middle Eocene Baltic amber fossils described in Agromyzidae at that time to other families. Although some additional amber fossils have since been listed as agromyzids (Poinar, 1992), the identification of these has not been confirmed. More recently, von Tschirnhaus and Hoffeins (2009) reviewed considerably more than 1,000 Baltic amber inclusions belonging to the Acalyptratae without noting the presence of agromyzid flies.

Fossilized leaf mines possibly attributable to Agromyzidae are more numerous, but care should be taken in interpreting these fossils. Based on published descriptions and illustrations, we cannot confirm an agromyzid origin for any of these fossils and suspect that many were not caused by agromyzid flies. One of the first such reported fossils, on a possible Ulmaceae leaf from the late Oligocene (Fig. 2.1), was reported as a mine of *Agromyza* sp. by Goeppert (1855). The mine is indeed similar to mines of the extant *Agromyza aristata* Malloch, 1915 on elm (Ulmaceae: *Ulmus* L.) in North America (Fig. 2.2), suggesting a long history for this species group. However, this case may serve as a cautionary tale; details of the frass trail were not figured or noted by Goeppert (1855), and we were unable to examine this specimen directly. Because mines made by *A. aristata* and those made by several species of *Stigmella* Schrank, 1802 (Nepticulidae) on *Ulmus* in Europe (Fig. 2.3) share several key features (length, degree of width increase, overall shape and trajectory, partial constraint by secondary veins), we cannot be sure that Goeppert’s illustration represents an agromyzid mine. Similarly, *Foliofossor cranei* Jarzembowski, 1989, was originally compared with agromyzid mines (Crane and Jarzembowski, 1980), but Kozlov (1988) suggested these mines from the Paleocene of the United Kingdom may be

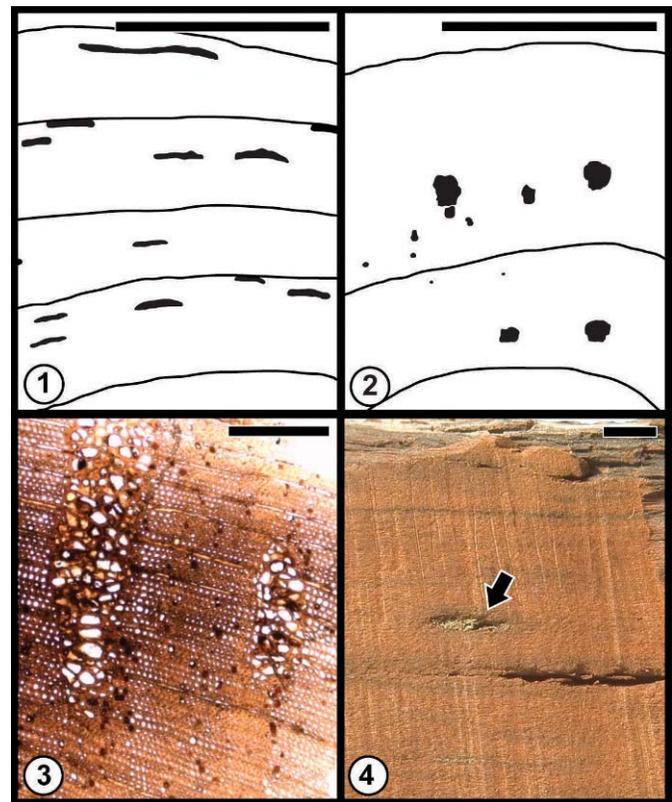


FIGURE 1—1–2, diagrammed cross-sections of tree trunks, showing characteristic feeding damage caused by an extant species of cambium-mining *Phytobia* Lioy, 1864 (Diptera: Agromyzidae) (1), and a species of *Opostega* Zeller, 1839 (Lepidoptera: Opostegidae; 2); 3–4, sections of fossilized woods showing analogous damage attributed to *Protophytobia cupressorum* Süss, 1979 on *Juniperoxylon silesiacum* (Prill) Kräusel (Cupressaceae; undet. Paleogene, Netherlands; section preparation SM.B 10934, Natur-Museum und Forschungsinstitut Senckenberg, Frankfurt), which is largely filled by secondary growth of modified tracheids (3), and at arrow, *Palaeophytobia salicaria* Süss, 1981 on *Populoxylon Mädel-Angeliowa* (Salicaceae; Pliocene, Germany; 4). Sources: 1–2 are reproduced from Kumada (1984); 3–4 were reimaged from original material illustrated by Süss (1979, 1980; in Geissert et al., 1981). Scale bars: 1–2 = 1 cm; 3 = 0.5 mm; 4 = 3 mm.

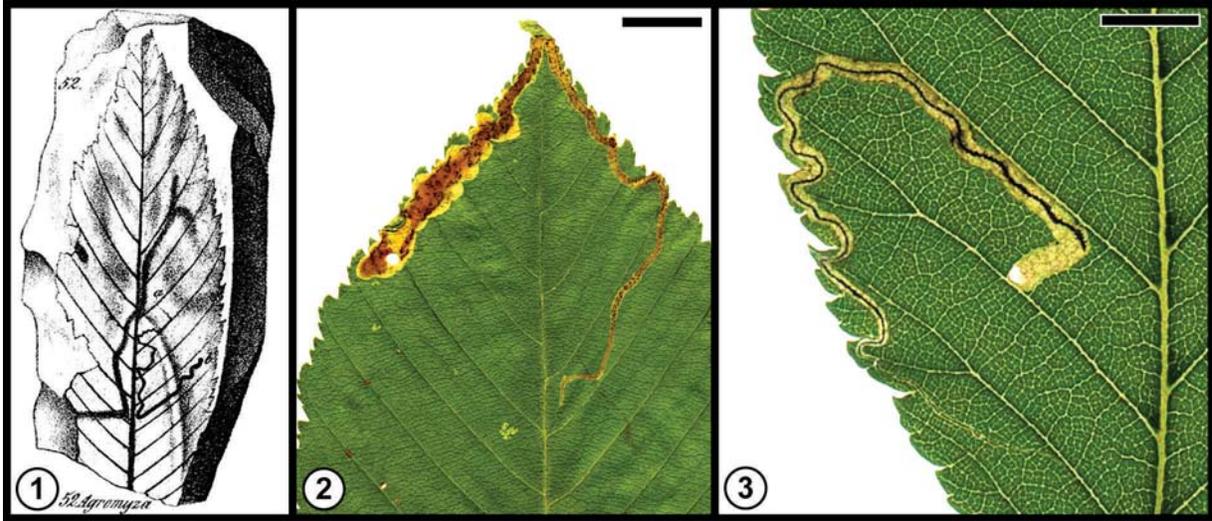


FIGURE 2—1–3, leaf mines on Ulmaceae showing the similar shape of mines caused by Diptera (2) and Lepidoptera (3) on the same host genus, for which details of the frass trail are often necessary to distinguish mines of these two orders. 1, Upper Oligocene fossil of a possible *Ulmus* leaf with a putative agromyzid leaf mine as figured by Goepfert (1855); 2, mine of the extant species *Agromyza aristata* Malloch, 1915 (Diptera) on *Ulmus americana* L. (note that some tissue has been removed near the mine terminus); 3, mine of *Stigmella ulmivora* (Fologne, 1860) (Nepticulidae, Lepidoptera) on *Ulmus* sp., courtesy of Willis (2009) (www.bladmineerders.nl). Scale bars: 2–3 = 5 mm.

lepidopterous in origin (see Jarzembowski, 1989). *Phytomyza lethe* Hering, 1930 was described as a leaf mine from the Miocene of Germany. Accurate generic placement is not possible, but Hering's experience with leaf-mining insects suggests that he may have correctly assigned it to Agromyzidae, although Hendel (1931–1936) was not convinced of this. Hering based his family assignment largely on the presence of a visible, semicircular exit slit at the end of the mine, which he suggests is diagnostic of dipteran larvae (Hering, 1951; but see below). A distinctive mine type, with a tightly looped, meniscate frass trail, was tentatively attributed to Agromyzidae by Berger (1949); this appears identical to the traces earlier reported as “*Phytoptus*” *antiquus* von Heyden, 1862 (see also Sittig, 1927; Labandeira, 2005). This generic assignment is a misattribution because *Phytoptus* Dujardin, 1851 is actually a genus of eriophyid gall-forming mites. Although these traces bear some resemblance to dipteran blotch mines, several lepidopteran miners produce similar frass trails, including several species of *Stigmella* (Nepticulidae). A few Agromyzidae may deposit frass in a similar pattern (Fig. 3.7, terminal portion of upper mine), but this is less common.

A number of Pliocene leaf mines were described by or cited in Straus (1967, 1977). Although the original illustrations are not sufficiently detailed, three of these (*Phytomyzites corni* Straus, 1977, *Phytomyza ranunculi fossilis* Straus, 1977, and *Phytagromyza populicola fossilis* Straus, 1977) are found on plants that are hosts of modern agromyzid species. Because of this, and considering their relatively recent origin, these traces can probably be assigned to recent genera, and they could even represent extant species on the same host plants. In contrast, two other ichnogenera tentatively assigned to Agromyzidae by Evenhuis (1994) (*Cuniculononus* Straus, 1977, and *Locononus* Straus, 1977) were in fact not assigned to any insect taxon in the original description, and probably do not represent agromyzid traces. There is likewise no indication that the Pliocene *Phytomyzites querci* Givulescu, 1984, is of dipteran origin, and we suspect a lepidopteran origin given the overwhelming predominance of lepidopteran miners on extant

Quercus L. (Fagaceae), which hosts only two extant agromyzid species (Spencer, 1990).

A distinctive, digitate and radiate blotch mine type (“asteronome”) with double rows of frass pellets was recently described by Krassilov (2008a; see also Krassilov, 2007, 2008b) from the Cretaceous of Israel as the ichnogenera *Asteronoma* Krassilov, 2008, with three included species. This mine type was suggested by Krassilov to represent a mine of dipteran origin, comparable to the extant *Phytomyza periclymeni* de Meijere, 1924 (Agromyzidae). However, we consider this resemblance to be more superficial; the consistently paired arrangement of “frass pellets” (i.e., directly opposite in the putative mine) contrasts with the alternating or more irregular arrangement seen in those extant agromyzid species that produce frass in discrete, separated spots. In addition, the early Late Cretaceous age of these traces (Turonian, ~90 Ma) is probably inconsistent with causation by agromyzids. An alternative possibility, mentioned in Krassilov (2007), is that these traces represent oviposition by damselflies. This is consistent with the inferred habitat (aquatic) and host plant (*Nehumbites* Berry, 1911, a plant with floating leaves) of at least some of the traces. In fact, somewhat similar traces were interpreted as oviposition marks by Krassilov (2008a, plate V). Other, similar paired rows of marks, including some in a radiate-digitate arrangement, are known from the Eocene Messel deposit in Germany on well-preserved leaf tissue with no evidence of leaf-mining (specimen SM.B Me 1396 on the monocotyledonous flowering plant *Araciphyllites tertarius* (Engelhardt) Wilde, Kvaček and Bogner, 2003). However, this damage more closely resembles paired mandibular puncture marks associated with surface fluid feeding, as known from chrysomelid beetle species (*Aulacoscelis* Duponchel and Chevrolat, 1843) on cycads (Windsor et al., 1999). Other leaf mines compared by Krassilov (2007, 2008a,b) to mines of extant Agromyzidae are possibly attributable to Diptera, but no substantial evidence of an agromyzid origin was presented for these traces.

A number of additional leaf mines reported in the literature have been compared with those formed by modern agromy-

TABLE 2—Selected references reporting undescribed fossil leaf mines compared with or ascribed to Agromyzidae. Status: NA – not accepted, U – uncertain or doubtful. Source: Labandeira (2005).

Reference	Locality/age	Host plant	Status	Notes
Goeppert (1855)	Germany [Oligocene]	<i>Ulmus</i> (Ulmaceae)	U	Similar to extant <i>Agromyza</i> on <i>Ulmus</i> , but also to species of <i>Stigmella</i> (Nepticulidae).
Berger (1949)	Bosnia [Miocene]	<i>Cinnamomum</i> (Lauraceae)	U	Continuous, meniscate line of frass possibly suggestive of Lepidoptera; similar to “ <i>Phytoptus</i> ” <i>antiques</i> .
Lang et al. (1995)	UK [Eocene]	various	U	Some mines compared to recent agromyzid analogs.
Labandeira (2002)	USA [Eocene]	<i>Aesculus</i> (Sapindaceae)	NA	Uniform, central frass trail; see fig. 4j of Labandeira (2002).

zids (Table 2). In many cases these associations were based on superficial resemblance in mine shape with those of a modern agromyzid analogue on a different host (Crane and Jarzembowski, 1980; Lang et al., 1995). We suggest that many leaf mines previously compared with or attributed to Agromyzidae probably were formed by Lepidoptera. Extant Lepidoptera show a broad variety of mine types, some of which closely resemble those of Agromyzidae in general form (Fig. 2.3). The pattern of frass deposition typically is more diagnostic, but it is extremely variable even within genera of Agromyzidae and Nepticulidae. Because leaf mine shape is often insufficient to distinguish between mines caused by larvae of Diptera and Lepidoptera, more specific features of the mine must be taken into consideration.

IDENTIFICATION OF AGROMYZID MINES

Despite the potential pitfalls, comparison of mines with those of known species can be very useful in identifying recent and fossil leaf mines. Hering (1951) provided a thorough general overview of leaf-mines and leaf-miner biology that reviews mine types and characteristics; systematic accounts of mining insects are found in Needham et al. (1928) and Hering (1957). Several excellent resources are available in print and on the World Wide Web that illustrate leaf mines from specific regions of Europe (Spencer, 1976; Csóka, 2003; Beiger, 2004; Ellis, 2007; British Leafminers, 2009). A few examples of the variety of leaf mines formed by agromyzid and lepidopteran leaf-miners are shown in Figure 3. Hering (1951) listed a number of characteristics helpful in attributing mines to one of the three major orders of mining insects. However, these traits mostly serve to identify the most distinctive mine types of each order, and will not aid in placing many common leaf mines.

The major functional difference between dipteran leaf-miners and those of other orders is the form of the mouthparts. Coleoptera, Lepidoptera, and Hymenoptera all have similar larval forms, with three anterior legs and various modifications of horizontal, chewing-type mandibles. These larvae feed with their dorsal or ventral body surface flush with the leaf epidermis. In contrast, dipteran larvae are legless, and the

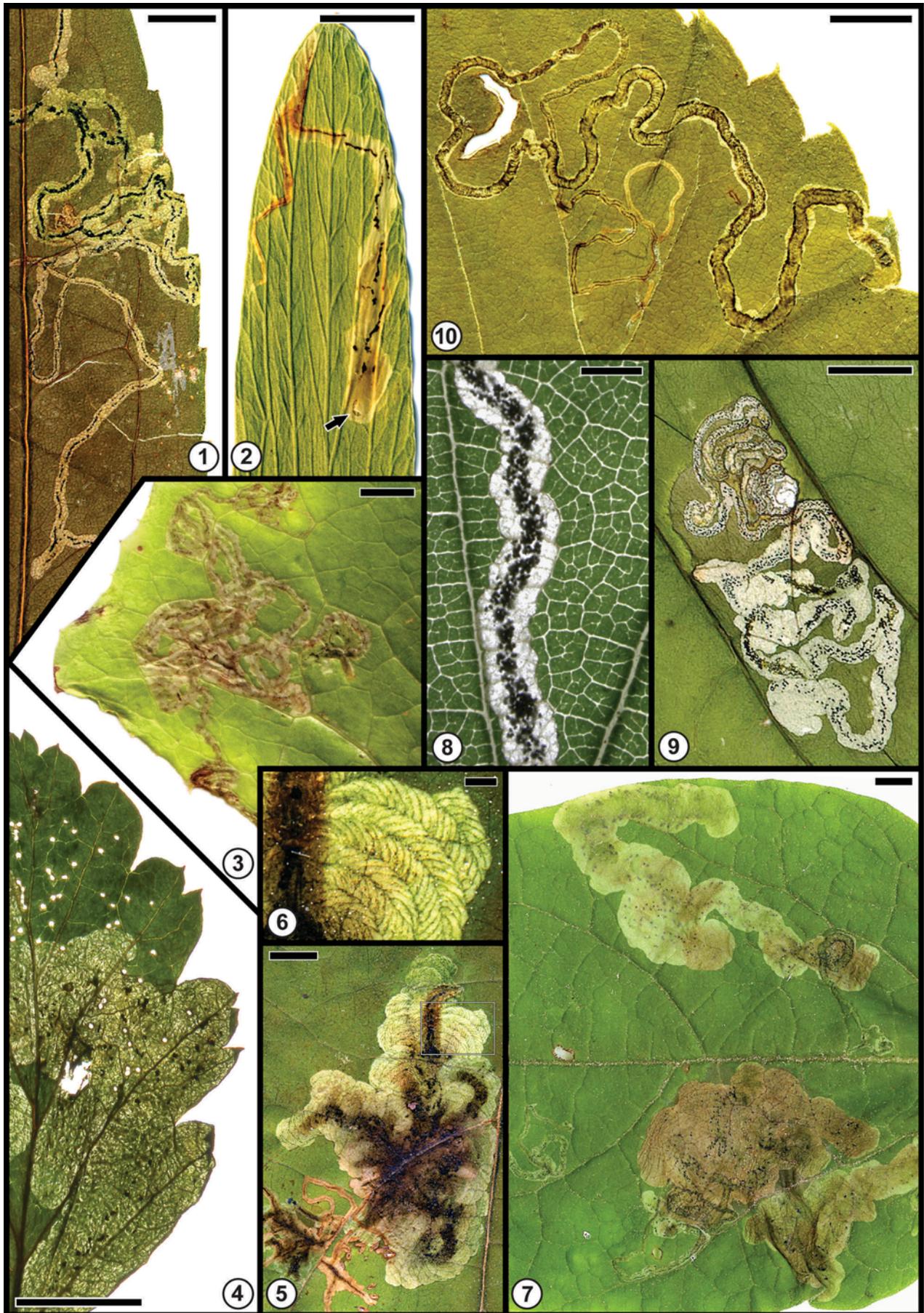
mandibles of most dipteran larvae, excluding lower dipteran leaf miners with horizontally working mandibles, are modified into “mouth hooks” which move in a vertical plane and are suitable for scraping or puncturing tissue and ingesting exuding fluids. Larvae of Agromyzidae are further distinctive in that they lay sideways in the mine, often alternating feeding between sides of the mine. This sideways body position is not present for most other leaf-mining Brachycera, and may be manifested in several details of the resulting leaf mine. In the discussion below, differences between agromyzid and lepidopteran leaf mines are discussed, but most are generally applicable to differences between dipteran mines and those of Lepidoptera, Coleoptera or Hymenoptera.

Mine shape.—Agromyzid leaf mines are generally classified into two main types: linear (or serpentine) mines, where the larva feeds primarily in a forward direction (but not necessarily in a straight line), and blotch mines, in which the larva feeds in multiple directions resulting in an irregular or ovoid mine (Hering, 1951). Many variations and combinations of these two types exist, and both are common among agromyzid species. Frequently, the details of mine shape are important in species identification. However, the shape and position of the mine often vary among related species, making generalizations about higher taxonomic categories difficult.

Although overall leaf-mine form is variable for both dipteran and lepidopteran leaf-miners, a few distinctive patterns may be indicative of one or the other. For example, some dipteran leaf miners form distinctive blotch mines, characterized as “ophiogenous” by Hering (1951), in which successive linear tracks are formed antiparallel and adjacent to previous ones, resulting in a distinctive “herringbone” pattern of primary and secondary feeding tracks (see Fig. 3.5–3.6). The form of these tracks is a consequence of dipteran mouthpart morphology, and is thus diagnostic of the order. This type is found in several agromyzid genera, though not particularly common, as well as in some leaf-mining Tephritidae. These distinctive feeding tracks, however, may be difficult to see in older, desiccated mines and would rarely enter the fossil record. Additionally, this type of mine is

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FIGURE 3—1–10, representative mines of six extant leaf-mining species of Agromyzidae (1–7) and, for contrast, three species of Lepidoptera (8–10). 1, serpentine mine of unidentified agromyzid on *Solidago* sp. (Asteraceae); 2, mine of *Liriomyza sativae* Blanchard, 1938 (Agromyzidae) on *Lathyrus* sp. (Fabaceae), showing alternation of frass bands and semicircular exit slit (arrow); 3, unidentified *Liriomyza* sp. (Agromyzidae) mining *Lactuca* sp. (Asteraceae); 4, blotch mine of *Agromyza* sp. (Agromyzidae) on *Holodiscus discolor* (Pursh, 1814) Maxim. with characteristic feeding puncture marks caused by the female ovipositor; 5–6, mine of *Phytoliriomyza melampyga* (Loew, 1869) on *Impatiens* sp. (Balsaminaceae) showing “herringbone” feeding marks diagnostic of some dipteran leaf-miners, enlarged in detail in 6; 7, blotch mines of *Amauomyza pleuralis* (Malloch, 1914) (Agromyzidae) on *Catalpa* sp. (Bignoniaceae); 8, closeup of frass trail of *Stigmella floslactella* (Haworth, 1828) (Lepidoptera: Nepticulidae) on *Corylus avellana* L. (Betulaceae), showing pelletized frass; 9, mine of *Mompha terminella* (Humphreys and Westwood, 1845) (Lepidoptera: Momphidae) on *Circaea* sp. (Onagraceae); 10, mine of unidentified Lepidoptera on *Vitis* sp. (Vitaceae). Images 8–9 are courtesy of Willis (2009), www.bladmineerders.nl. Scale bars: 6, 8 = 1 mm; others = 5 mm.



mostly observed on herbaceous plants. Another distinctive pattern, termed an “asteronome” by Hering (1951), occurs when larval feeding centers on the leaf midrib or other vein, with radial offshoots into other parts of the leaf. This type of mine is most common among Diptera; several agromyzids, including *Phytomyza periclymeni*, exhibit this feeding type, as do some Anthomyiidae, Drosophilidae, and other dipteran miners.

Many Agromyzidae, especially as small larvae, tend to produce narrow, irregular serpentine mines that abruptly change direction and often overlap with earlier traces (Fig. 3.3). In some cases, this kind of mine appears blotch-like or expands to become a blotch mine, but this pattern may also extend into later instars or be followed by a more regular linear mine. Linear mines of Lepidoptera, though often wandering, tend to be less irregular, and rarely overlap with earlier traces. Although this difference is more subjective, it can be useful in establishing a “gestalt” for dipteran leaf-mines.

Frass deposition.—The disposition of frass in the mine is often a valuable clue in determining the identity of the miner. Most importantly, because dipteran leaf-miners do not ingest cell walls, they produce a fluidized frass that hardens to form dark specks or a dark coating on plant tissue in the mine interior. Lepidoptera and other leaf-miners, in contrast, nearly always produce solid frass, usually in discrete pellets. Among rare exceptions, Hering (1951) mentions some sap-feeding epidermal miners among the Lepidoptera, such as *Phyllocnistis labyrinthella* Bjerkaner, 1790 (Gracillariidae). This difference is not always apparent externally in fresh material, but if the mine is dissected under a microscope, usually it can be readily ascertained. Pelletized frass is sometimes discernable in fossil lepidopteran mines, although the frass grains may become distorted and appressed during diagenesis into a threadlike trace, making determination of the causative agent more difficult.

The pattern of frass deposition can be just as important in determining the origin of a leaf mine, especially for linear mines. Because agromyzid larvae lay on their sides and usually alternate between sides of the mine to feed, the resulting spots or strips of frass often alternate in linear mines. For some Agromyzidae this alternation of frass lines or spots is readily apparent throughout the course of the mine (Fig. 3.2), while for others it may only occur for a short stretch of the mine, with a more irregular, sometimes medial frass line for the remaining length (Fig. 3.1). In other Agromyzidae (especially *Agromyza* Fallén, 1810), the frass is more irregularly dispersed in small specks throughout the mine or in rows at either side (Fig. 2.2). In these cases, alternation of frass specks may be apparent near the beginning of the mine only or not at all. For example, in *Phytomyza agromyzina* Meigen, 1830 and *Aulagromyza luteoscutellata* (de Meijere, 1924) a wide, central band of frass specks is formed in the mine (Spencer, 1976), a pattern more typical of lepidopterous mines. Although not present in all cases, an alternating frass pattern is a strong indicator of agromyzid origin. In contrast, lepidopteran leaf miners often form a single line of frass in the center of the mine, or alternatively disperse the frass more evenly throughout the leaf mine width, (Hering, 1951; see Fig. 2.3, Fig. 3.8–3.10). A few Lepidoptera deposit frass external to the mine, leaving the mine free of frass. Frass deposition in blotch mines is more difficult to characterize, often making identification of the miner taxon problematic, but frass is often clumped in the center or side of the mine when formed by Lepidoptera, and also Anthomyiidae and the agromyzid genus *Calycomyza* Hendel, 1931 among the Diptera. Hymenopteran sawfly

miners generally produce pelletized frass which is unattached and desiccates in the mine, accumulating at the mine margin.

Exit slit or pupation mode.—Hering (1930, 1951) emphasized the presence of a semicircular exit slit as indicating dipteran origin of a leaf mine, for both linear and blotch mines. This character does not seem to be as useful as Hering suggests, but most agromyzid leaf-miners do exit the mine via a semicircular slit (Fig. 3.2). According to Hering (1951), most non-dipteran leaf miners exit the mine via circular holes (small in Lepidoptera and large in Coleoptera and Hymenoptera). However, semicircular exit slits very similar to those of Agromyzidae are also commonly formed by species of *Stigmella* (Nepticulidae), *Phyllocnistis* (Gracillariidae) and some other Lepidoptera (Needham et al., 1928; Beiger, 2004; Don Davis, personal commun., 2009). Furthermore, the exit slit can be difficult to see, even in fresh material, and may rarely be visible in fossil mines; for example, Lang et al. (1995) were not able to observe an exit slit in any of 29 studied leaf mine fossils. Hering’s (1930) observation of the exit slit in the fossil *Phytomyza lethe* may be an exceptional case.

A number of species of Agromyzidae (especially of *Phytomyza* Fallén, 1810 and *Cerodontha* Rondani, 1861; Winkler et al., 2009a) and a few Lepidoptera (Fig. 3.10; e.g., some Gracillariidae) undergo the pupal stage still embedded in the leaf tissue instead of exiting to pupate in the ground. Because the mode of pupation and the shape of the pupa (or puparium in Diptera) differ between these orders, identification will usually be straightforward in these cases. Specifically, pupating Lepidoptera are usually enclosed by an elongate, silken cocoon, beneath which external appendages are present; higher Diptera (Cyclorrhapha) are enclosed during the pupal period in an ovoid puparium with few external features, formed from the hardened skin of the final instar larva.

Other dipteran miners.—Mines of other dipteran leaf miners are less common and usually not confused with agromyzid mines. Those of the “lower Diptera” (e.g., Chironomidae, Tipulidae, Sciaridae) are especially distinctive (narrowly and uniformly linear, sometimes branching), and less frequently encountered. Ephydrid leaf miners (*Hydrellia* Robineau-Desvoidy, 1830) mostly mine aquatic or semiaquatic plants which are not hosts of Agromyzidae (Deonier, 1971). Tephritidae (tribe Trypetini), Scathophagidae, and Anthomyiidae usually form large blotch mines in herbs (never trees), sometimes with multiple larvae; in earlier stages, these may be mistaken for agromyzid mines. However, the large size of the mature larva (mostly > 4 mm) is usually indicative. Leaf-mining species are scattered in several other brachyceran Diptera families (e.g., Phoridae, Dolichopodidae, Syrphidae, Drosophilidae, Chloropidae; see Needham et al., 1928; Labandeira, 2005), but most are rarely-encountered, exceptional species, or very specific in their habits and host choice (e.g., grass-mining Chloropidae). Due to their relative rarity and derived phylogenetic position within their respective families, and because of their absence on woody host plants, dipteran leaf-miners other than Agromyzidae are less likely to be encountered in the fossil record.

Summary.—In short, an agromyzid attribution can be securely diagnosed by the presence of fluidized frass in intermittent bands or specks, alternating between the two sides of the mine. Probable agromyzid attribution for recent leaf mines is indicated by: 1) fluidized frass in any configuration except a uniform medial line if the host is arborescent; 2) blotch mines with a distinctive antiparallel (“herringbone”) pattern; or 3) (less decisively) irregularly winding serpentine mine shape, especially in early stages, with

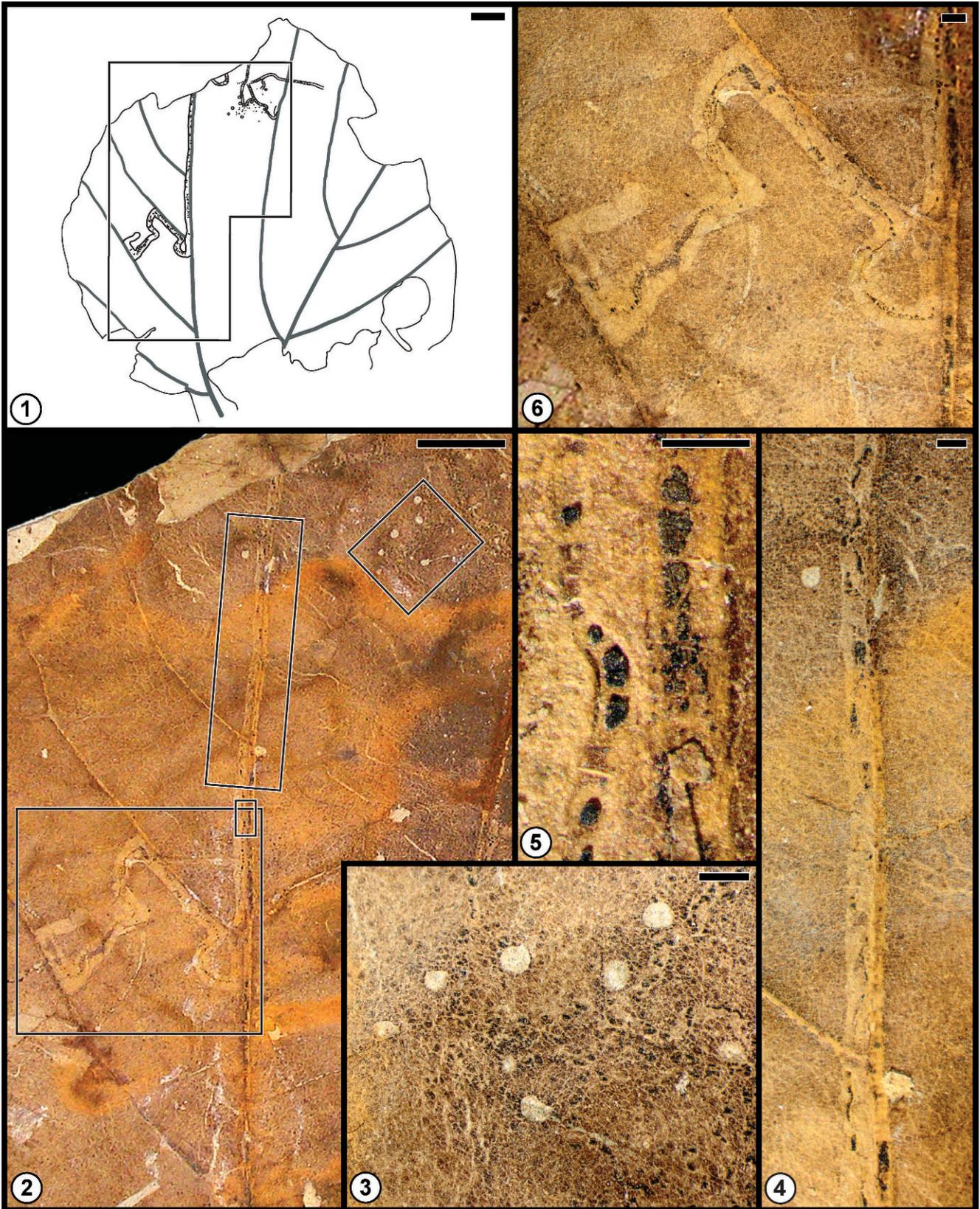


FIGURE 4—1–6, *Phytomyzites biliapchaensis*, nov. ichnosp., holotype specimen (USNM 539754) on *Platanus raynoldsii* Newberry, 1868 (Platanaceae), from the Powder River Basin of Montana (early Paleocene). 1, drawing of whole leaf showing location of mine; 2, entire mine, magnified from 1, showing areas that are additionally magnified in 3–6; 3, close-up of feeding punctures analogous to those formed by the ovipositor of extant female Agromyzidae; 4, segment from middle portion of mine, showing alternating frass bands characteristic of agromyzid leaf miners; 5, detail of channelized frass depression, with fluidized frass flakes adjacent to the secondary vein; 6, end of mine, with frass absent in the terminus region. See descriptions of fossil agromyzid mines in the text for additional details. Scale bars: 1, 2 = 1 cm; 3, 4, 6 = 1 mm; 5 = 0.5 mm.

subsequent mine traces overlapping or closely approximating previous ones. Most leaf mines in extant herbs are caused by agromyzids, but a non-agromyzid origin can usually be assumed when any of the following apply: 1) frass in distinct pellets (not just separate, circular spots or flattened lumps), 2) frass deposited in a uniform, narrow medial line; 3) mines uniformly narrow (<1 mm), not widening appreciably in early stages, and no wider than width of the larva for the entire length of mine; 3) host plant an aquatic herb (except those belonging to the order Poales); and 4) (in most cases) large blotch mines with larvae > 5 mm in length. Although the above characteristics are not always sufficient to confidently distinguish mines of Agromyzidae from those of other insects, this often will be possible, especially for linear mines. The general applicability of these criteria to extinct agromyzid species is assumed, but of course depends partly upon the constancy of broad-scale host use patterns. Furthermore, confident identification for fossil material will depend on whether details such as the frass trail are well-preserved.

SYSTEMATIC PALEONTOLOGY

Family AGROMYZIDAE Fallén, 1810

ICHNOGENUS PHYTOMYZITES Straus, 1977

Type species.—*Phytomyzites corni* Straus, 1977

Other species.—*Phytomyzites querci* Givulescu, 1984 (assignment doubtful)

Emended diagnosis.—Leaf mines of variable shape, but having linear or irregular serpentine form during at least early stages. Frass trail fluidized, intermittent, in small specks or in segments of variable length, which may be in the center of the mine, but usually alternating at sides for some portion of the course; or frass trail consisting of irregular fluidized specks dispersed across mine width or at both sides of mine. Terminal portion of mine free of frass. Sometimes associated with small (0.5–1.0 mm) circular holes, surrounded by darker reaction tissue.

Discussion.—The ichnogenus *Phytomyzites* was originally proposed by Straus (1977) for *P. corni*, a Pliocene leaf mine on *Cornus* L. probably comparable to that made by the extant *Phytomyza agromyzina* Meigen on *Cornus* today. The original (Latin) diagnosis of *Phytomyzites* is brief and relatively uninformative: “This insufficiently preserved fossil is named *Phytomyzites*, because of its closeness in appearance to the genus *Phytomyza* or related genera.” Because leaf mine shape is variable within genera of Agromyzidae and mine characteristics are rarely sufficient to diagnose extant genera, we propose that the concept of *Phytomyzites* be expanded to include all fossil leaf mines of the linear or linear-blotch type demonstrably caused by agromyzid flies. We have accordingly emended the diagnosis above.

PHYTOMYZITES BILIAPCHAENSIS Winkler, Labandeira and Wilf, new ichnospecies

Figures 4.1–4.6, 5.1–5.4, 6.1–6.4, 7.1–7.5

“Elongate, serpentine, agromyzid dipteran mine (DT104)”
Wilf, Labandeira, Johnson and Ellis, 2006, p. 1114, fig. 1A.

“Damage Type 104” Labandeira, Wilf, Johnson and Marsh, 2007, p. 12

unnamed “fossilized leaf mines” of Agromyzidae, Winkler, Mitter and Scheffer 2009, p. 1, fig. 1D–E.

Diagnosis.—Early stages approximately 0.5 mm in width, winding irregularly, with irregular deposition of frass across the width of the mine. Later segments linear or serpentine, rarely crossing major veins, widening to 1.5 mm or more in width at terminus. Frass trail mostly within a narrow channel, depressed from surrounding tissues. This frass channel often central but alternating at sides for at least some portion of the mine. Terminal portion of mine with semicircular margin, free of frass for last 5 mm. Total length of mature mine greater than 5 cm. Other features as for genus.

Description.—

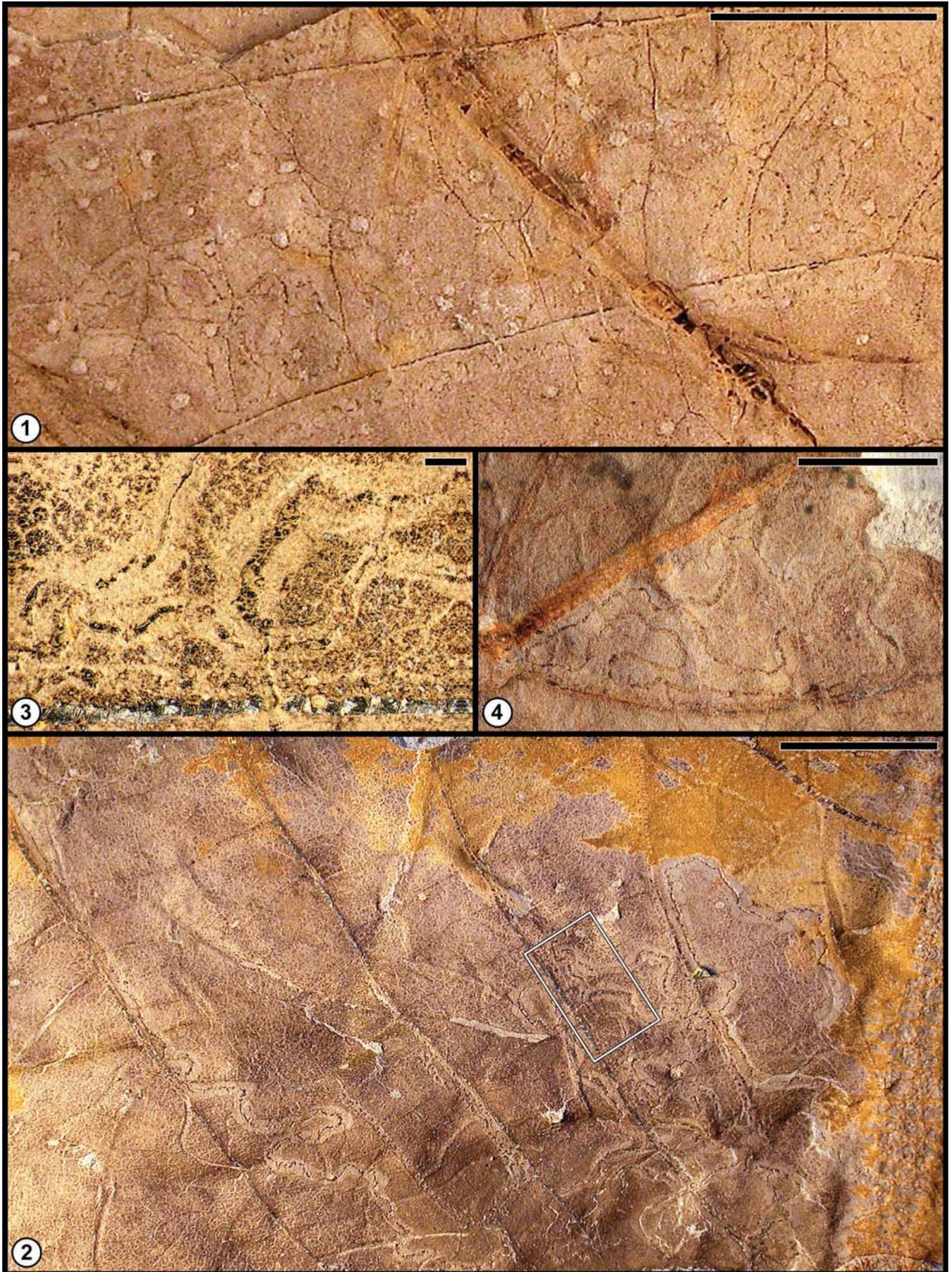
Holotype: USNM 539754 (Fig. 4.1–4.6) – Mine on *Platanus raynoldsii* Newberry, 1868 (Platanaceae), consisting of two sections made discontinuous by missing portion of substrate near edge of leaf. Initial section consisting of indistinct, meandering traces, about 0.5 mm wide, in the apical portion of the leaf, approximately 2 cm from the inferred leaf margin. Some of these form sublinear segments of 2 cm or more. Irregular dark flakes of fluidized frass present, initially closely spaced and extending over half the width of the mine, later up to 1 mm or more apart. Seven or more distinct, subcircular penetration features (holes) present (diameter 0.5 – 0.7 mm) among initial portion of mine, surrounded by dark reaction tissue (Fig. 4.3). Second section begins from chipped edge of substrate near the inferred leaf margin, and continues linearly adjacent to major leaf vein for 5 cm. Subsequently, mine consists of six segments (two curved and four straight, two of which follow secondary leaf veins) of 0.5 to 1.2 cm in length, joining at nearly right angles (Fig. 4.6). Width of mine just under 1 mm at edge, widening to nearly 1.5 mm at terminus, which ends in an ovoid chamber with a semicircular terminal margin. No exit slit is visible. In first 2 cm, bands of dark, fluidized frass not in visible channel, alternating between sides of the mine (Fig. 4.4), subsequently intermittent in narrow (up to 0.5 mm wide), recessed channel which is mostly near the center of the mine (Fig. 4.5). Terminal 5 mm of mine, including final linear segment and terminal chamber, free of frass.

Paratypes (also on *Platanus raynoldsii*):

USNM 539755 (Fig. 5.1) – One or more meandering mines with indistinct boundaries, approximately 1 mm wide, with mostly distinct, very narrow central frass channels. Mined tissue mostly in area (approx. 2 cm × 5 cm) bounded by two secondary leaf veins. Numerous (~50) more or less distinct subcircular holes scattered among mines and other parts of the leaf fragment, from 0.5 to 1.0 mm in diameter. No distinct origin or terminus evident.

USNM 539756 (Fig. 5.2–5.3) – Two separate mines on a single leaf fragment. First mine (Fig. 5.2, at left) with origin indistinct, but some early portions of mine clearly evident. Early segments of mine approx. 0.5 mm wide, in two major

FIGURE 5—1–4, *Phytomyzites biliapchaensis*, paratype and additional referred specimens, on *Platanus raynoldsii* (Platanaceae), from the Powder River Basin of Montana (early Paleocene). 1, USNM 539755, showing numerous ovipositor punctures among indistinct leaf mines; 2, USNM 539756, illustrating the linear to highly winding trajectory of two extensive mines; 3, USNM 539756, showing magnified detail of a mine from 2, including frass flakes; 4, USNM 539757, exhibiting the control of primary venation on mine course development. Additional descriptions and details of fossil leaf mines are provided in the text. Scale bar 1, 2, 4 = 1 cm; 3 = 1 mm.



linear segments of over 1 cm; one of these along a minor leaf vein, and appearing to consist of two adjacent trails. Frass in early segments more or less evenly spaced, about 0.7 mm apart. After leaving leaf vein, mine gradually widens to about 1 mm, after which distinct frass channel is present. Subsequently, mine wanders for approximately 2 cm and follows a leaf vein for another 1 cm before becoming indistinct. Final visible portion of mine about 1 mm wide. Second mine (Fig. 5.2, at right) considerably more meandering, often approaching or adjacent to earlier traces, and also including both early stage (0.5 mm width) and late stage (up to 1.5 mm) traces. Mine appears to terminate in an indistinct, ovoid chamber, with the last 5 mm free of frass. Otherwise, frass and frass channel as in first mine (see detail, Fig. 5.3).

USNM 539758 (Fig. 6.1–6.2) – Short segment of mine showing extensive looping, typical segmented frass trail, region of host-plant discoloration along mine edge, and expansion of the frass trail at bottom, enlarged at lower left. Region of expansion evidently consists of transverse swaths of frass deposition that occupy almost the entire mine width and providing a distinctive carbonized pattern.

USNM 539758 (Fig. 6.3) – Another mine region on same slab surface as above, showing characteristic mine looping, frass trail segmentation, host-plant discolored zone and control of trajectory by major venation and not minor venation.

USNM 539937 (Fig. 7.4) – The figure shows an overlay drawing of this specimen with circular penetration features, emergent mines, and other, longer mines. Note the lack of frass in the initial mine. Mine course controlled by primary and secondary venation, occasionally by tertiary venation, and not by lower-ranked veins.

Etymology.—*Phytomyzites* = pertaining to *Phytomyza* (or other agromyzid genera); *biliapchaensis* derives from the Apsáalooke (Crow Indian) name for the Powder River, Biliapchaashe, meaning “Ash (biliapcha) River (ashe).”

Types.—Holotype, USNM 539754, and all paratypes (USNM 539755, 539756, 539758, and 539937) are from the Mexican Hat locality, USNM locality 42090, located in the Powder River Basin, Custer County, southeastern Montana (N 46°25'53", W 105°14'28", WGS84 datum). The quarry is in the Lebo Member of the Fort Union Formation, and corresponds to strata dated at between 64.0 and 64.7 Ma by Belt et al. (2004).

Other material referred.—

USNM 539757 (Fig. 5.4) – Winding mine in angle formed by one primary and one secondary leaf vein, with the mined area extending for about 2.5 cm from origin of secondary vein. Width in discernable segments 1 mm – 1.8 mm, width of frass channel approximately 0.2 mm. No distinct origin or terminus visible.

USNM 539759 (Fig. 6.4) – Long, extensive development of two mines exhibiting convoluted mine trajectory, control of major veins, and segmented nature of the frass trail; note

occasional crossing of primary venation along mature segments of mine paths.

USNM 539760 (Fig. 7.1) – Highly sinusoidal mine at angle of two primary veins, showing the control of primary and secondary venation on mine trajectory and the comparative inconsequence of tertiary and quaternary venation. Mine terminus slightly beyond upper-right corner.

USNM 539935 (Fig. 7.2) – Extensive mine with two scales of sinuosity, showing intermittently concentrated fluidized frass trail. Note control of primary and secondary venation on mine course.

USNM 539936 (Fig. 7.3) – Region of three subcircular surface penetration features incompletely penetrating the leaf-blade thickness, with surrounding reaction-tissue rims. Circular structures are positioned on minor veins or in nonveined leaf regions often near mines on this host.

USNM 498154 (Wilf et al., 2006, fig. 1A) – Long, extensive mine (>5 cm) with two antiparallel segments adjacent to major vein, and one segment looping away from major vein.

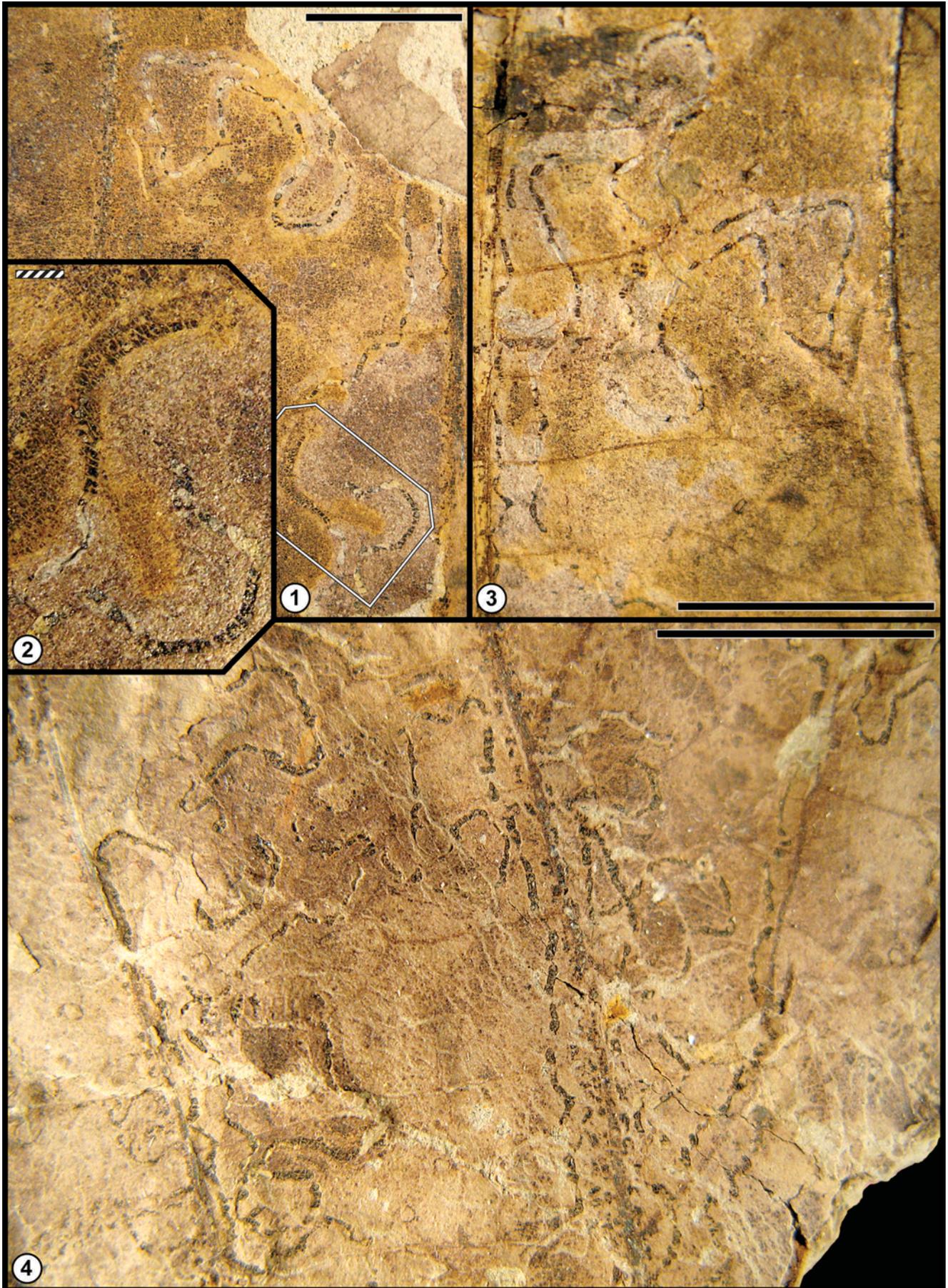
Occurrence.—All type and referred specimens are from the plant-fossil collection made at the type locality by PW and CCL in 2004 and reported by Wilf et al. (2006). The presence of abundant fossilized leaf mines on host plants at this locality was first noted by Lang (1996) and subsequently discussed by Wilf et al. (2006). The Mexican Hat plant-fossil site was first described by Williams (1988); other relevant literature includes Diemer and Belt (1991) and Manchester and Dilcher (1997). In addition to the large collection under USNM loc. 42090, plant-fossil collections from Mexican Hat are housed at the Peabody Museum, Yale University (see Manchester and Dilcher, 1997) and the Denver Museum of Nature and Science (DMNH locality 1251).

Host plant.—All type and referred leaf mines are on *Platanus raynoldsii*, an extinct species of Platanaceae.

Discussion.—These leaf mines were first reported by Wilf et al. (2006) as having an agromyzid origin, though no formal description was given, and they are assigned to “damage type 104” in that paper and in the morphotyping system of Labandeira et al. (2007). The assignment was based on the distinctive, intermittent fluidized frass trail, which distinguishes them from other fossil leaf mines, most lepidopterous in origin, studied by these authors. Winkler et al. (2009b) examined the same material and briefly proposed other characteristics that, considered together, allow confident attribution of these trace fossils specifically to Agromyzidae. These characters, discussed in more detail above, include alternation of the frass trail at the sides of the mine for some portion of the mine.

Confident attribution of *Phytomyzites biliapchaensis* to agromyzid larvae is further indicated by the subcircular holes found in most of the Mexican Hat fossils. These are identical to ovipositor marks formed by females of extant species of Agromyzidae (Fig. 3.4), and identical marks are not formed by any other leaf-mining taxon. Although eggs are deposited

FIGURE 6—1–4, *Phytomyzites biliapchaensis*, nov. ichnosp., additional paratype and referred specimens, on *Platanus raynoldsii* (Platanaceae), from the Powder River Basin of Montana (early Paleocene). 1, USNM 539758, a tightly sinusoidal mine adjacent to a primary vein, showing a typical trajectory of fluidized, segmented frass surrounded by a discolored zone presumably representing insect feeding; 2, USNM 539758, enlarged area from the template at 1, showing transverse expansion of frass trail, attributable to a wider swath of frass deposition; 3, USNM 539758, a mine showing the irregularly segmented nature of the frass trail; 4, USNM 539759, a mine exhibiting several frass-trail crossovers and control of the trajectory by primary and secondary host-plant venation. See descriptions of fossil agromyzid leaf mines in the text for additional details. Scale bars: 1, 3, 4 = 1 cm (solid pattern); 2 = 1 mm (hatched pattern).



in a few such punctures, in most cases the female instead walks backward to imbibe the emerging liquid. This feeding behavior is known to affect female survival and fecundity (Zoebisch and Schuster, 1987; Scheirs et al., 2000), but it probably also allows the female to evaluate the plant as a potential host for her offspring (Parrella, 1987). For example, Sehgal (1971) noted that mature females of the narrowly oligophagous *Phytomyza pullula* Zetterstedt, 1848 (as *P. matricariae* Hendel, 1920) made only a few punctures in plants unrelated to usual hosts (without oviposition), but the number of punctures increased greatly in plants closely related to the usual hosts. In the field, multiple ovipositor puncture marks are not always present on leaves with mature leaf mines, and if present the marks may be minute and inconspicuous. The reaction of the host plant seems to be important in determining the size of the marks. For instance, agromyzid species that typically emerge early in the season and oviposit on young, tender leaves, such as many of the species feeding on trees and grasses, often create prominent puncture marks as these expand to form conspicuous holes when the leaf grows. This appears to be the case with the punctures accompanying fossils described here.

Examination of further material (about 100 mined *Platanus raynoldsii* leaves) from the same locality confirmed that the circular marks are strongly associated with mines of *P. biliapchaensis*. These marks, appearing in clusters or as single occurrences, are nearly always found near mines, though several exceptions to this were observed. Furthermore, each leaf mine was associated with one or more puncture marks. In a few instances, the origin of leaf mines could even be traced to a specific puncture (oviposition mark), though in most cases the mine origin was not apparent. Overall, mines apparently originate from about five percent of punctures, a figure roughly consistent with the proportion of feeding punctures to oviposition punctures observed for extant Agromyzidae (Parrella, 1987).

The distinctive frass channel that characterizes these fossils is somewhat puzzling, and we have not seen an analogue in extant leaf mines. This channel is evident in both part and counterpart of the fossils, and thus seems to represent a tubular cavity; however it is much narrower than the boundary of the discolored, mined area. Most likely this mine channel was positioned internally within the plant-host tissues, and the preserved leaf blade is cleaved through the central tissue area. This split reveals internal mine details and not the surface, epidermal expression of the deeper-seated mine. This preservation is typical for leaf mines but not for more solid three-dimensional structures such as galls.

Because details of leaf mines are so variable within agromyzid genera, we cannot attribute the fossil traces reported here to any particular genus or even subfamily of Agromyzidae. Indeed, it is possible that they represent an extinct lineage. The variable shape and trajectory of these mines further highlight the inadvisability of identifying or attributing leaf mines to certain recent taxa based on the shape of the mine alone. Most extant agromyzid species have some

stereotypical feeding behaviors that allow separation based on mine shape compared to species feeding on the same host. These behaviors, however, often vary between closely related species. Moreover, mine shape is known to vary within some agromyzid species, and may differ significantly on host plants of different leaf size or architecture (Scheirs et al., 1997). Furthermore, the pattern of frass deposition varies across life stages in *P. biliapchaensis*. This variation is also observed in mines of some recent Agromyzidae. For example, in *Amauromyza pleuralis* (Malloch) (Fig. 3.7), an early meandering linear mine has tiny frass specks evenly distributed across the width of the mine, and this abruptly widens to an elongate blotch mine with sparsely scattered frass flecks. An analogous transition is observed in early mine segments of one paratype of *P. biliapchaensis* (USNM 539758, Fig. 6.2).

PHYTOMYZITES SCHAARSCHMIDTI Wappler, new ichnospecies
Figures 8.1–8.8

Diagnosis.—Early stages approximately 0.1–0.2 mm in width, winding irregularly. Later segments linear or serpentine, rarely crossing major veins, widening to 0.3 mm in width at terminus. Terminal portion of mine semicircular, free of frass for last 1.2 mm. Frass bands initially central, alternating at sides in the terminal portion of the mine. Other features as for genus.

Description.—Mine on *Toddalia ovata* Wilde, 1989 (Rutaceae) with distinct origin on secondary vein. Complete mine tightly sinusoidal with minimal width increase (0.19–0.28 mm). Estimated total length 5.28 mm. Initially, fluidized frass present, closely spaced, and extending over full width of the mine (Fig. 8.4), depressed from surrounding tissues, separated in three sections. Near terminus, bands of dark, fluidized frass alternating between sides of the mine (Fig. 8.5–8.6). Mine appears to terminate in a distinct, ovoid elongated chamber (Fig. 8.7–8.8), with the last 1.04 mm free of frass. Approximately 0.5 mm before the mine terminus is an indistinct body (arrow, Fig. 8.7), possibly representing fragments of a puparium or larval remains.

Etymology.—The specific epithet honors the late Prof. Friedemann Schaarschmidt of the Senckenberg Museum for his work on the Messel paleoflora.

Types.—The holotype (Messel specimen SM.B Me 822; Fig. 8.1–8.8) was collected at the Grube Messel near the town of Darmstadt (Hesse, Germany). The fossil specimen was found in the Messel Formation (lower Middle Eocene, lowermost Geiseltalian, Mammal Paleogene level 11) in grid square E8/9, above local stratigraphic marker level Alpha. The sediments of the Messel Pit were deposited in a deep maar lake created by explosive volcanic activity (Schulze et al., 2002; Felder and Harms, 2004). Radiometric dating of basalt fragments underlying the fossiliferous sediments indicate an age of about 47.8 Ma (Mertz and Renne, 2005).

Occurrence.—Not known from localities other than the type locality (Messel).

Host plant.—*Toddalia ovata*, a fossil species of Rutaceae.

FIGURE 7—1–5, *Phytomyzites biliapchaensis*, nov. ichnosp.: additional paratype and referred specimens, on *Platanus raynoldsii* (Platanaceae), from the Powder River Basin of Montana (early Paleocene). 1, USNM 539760, a nearly complete mine in the area between a primary and secondary vein, showing a tightly sinusoidal trajectory; 2, USNM 539935, a broadly looping mine showing a segmented frass trail and a discolored zone presumably representing the path of mined tissue; 3, USNM 539936, circular ovipositor marks (feeding punctures, white arrows) with surrounding reaction tissue, typical of agromyzid leaf miners; 4, USNM 539937, examples of circular ovipositor marks among incipient mines; 5, USNM 539937, overlay drawing of vein-controlled linear mines amid 14 ovipositor marks (black arrows), two of which (white arrow) are adjacent to but are not connected to agromyzid mines, indicating the subsequent emplacement of ovipositor punctures after linear mines were established. See the descriptions of fossil leaf mines in the text for additional details. Scale bars: 1, 2, 4, 5 = 1 cm (solid pattern); 3 = 1 mm (hatched pattern).



Discussion.—*Toddalia* includes a single extant species (*T. asiatica*) that occurs throughout tropical Africa and Madagascar, the Indian subcontinent, southeast Asia, Indonesia, northern Australia, Philippines and adjacent southwestern Pacific archipelagos, and typically occurs in forests near rivers or streams (Gregor, 1979). The host plant identity was determined earlier by Wilde (1989), who performed cuticular analysis of this specimen. The mine of *P. schaarschmidti* described here is typical of many extant Agromyzidae, such as members of the genus *Liriomyza*. Attribution to Agromyzidae, however, is mainly based on the presence of distinctive, alternating bands of frass (compare Fig. 3.2). The structure located near the mine terminus could be interpreted as the remains of a puparium, indicating internal pupariation. This behavior is found in a number of unrelated Agromyzidae (Winkler et al., 2009a); however, the puparium is usually situated at the mine terminus. A more likely possibility is that this feature represents a larva that died before reaching maturity; this also could be indicated by the extremely small size of the mine. Larval mortality is a common occurrence in extant Agromyzidae, presumably due to larval parasitoids or failure to overcome host chemical defenses. A number of other mine morphotypes were found on *Toddalia* at the same locality, at least some of which are suggestive of lepidopterous feeding due to having pelletized frass in the center of the mine.

EVOLUTIONARY IMPLICATIONS

Our findings are significant in establishing a minimum age for Agromyzidae, but they also have broader implications for fly evolution and plant associations. Most importantly, *Phytomyzites* confirms a minimal early Paleocene or possibly Late Cretaceous origin for schizophoran (“higher”) flies, the diverse clade of approximately 85 families to which agromyzids and other related “acalyptrate” flies belong. Schizophora, and Agromyzidae in particular, long has been considered a Cenozoic radiation (Rohdendorf, 1974; Wiegmann et al., 2003; Grimaldi and Engel, 2005), and some have suggested that major diversification did not take place before the Miocene (Wilson, 1978; Blagoderov et al., 2002). The identity and/or age of the only two putative schizophoran fossils from the Cretaceous are ambiguous (Grimaldi and Engel, 2005): a presumptive calyptrate puparium from the latest Cretaceous of Canada (McAlpine, 1970), and an earlier specimen from New Jersey amber tentatively identified as the acalyptrate family Milichiidae (Grimaldi et al., 1989). Few, if any, confirmed reports of schizophoran fly fossils from the Paleocene exist. More than 20 schizophoran families have their earliest fossil records from middle Eocene Baltic amber (Hennig, 1965; Evenhuis, 1994; von Tschirnhaus and Hoffeins, 2009). The phylogenetic position of Agromyzidae within Schizophora is not well understood (Winkler et al., 2010), and it is possible that this clade, based on phylogenetic position, represents an early-branching lineage from the Late or latest Cretaceous.

Regarding host plant evolution, we note that species of Platanaceae are not recorded as host plants for any living leaf-mining Agromyzidae (Benavent-Corai et al., 2005). Only three highly polyphagous species have been found feeding on Rutaceae—the widespread *Phytomyza horticola* Goureau, 1851 on *Ruta* L. in Europe, and two species of *Tropicomyia* Spencer, 1973 on *Citrus* L. and *Murraya* L. in Nigeria and Australia (Spencer, 1990). Although each of these three species form puparia inside of the leaf mine, as possibly observed in *P. schaarschmidti*, none is likely to be related to this trace fossil—*P. horticola* was probably derived from Asteraceae-feeding

ancestors in the last 10 Ma (Winkler et al., 2009a, 2009b), and *Tropicomyia* species form distinctive surface (epidermal) mines, usually with no visible frass deposits (Spencer, 1973). No agromyzid mines have been reported from *Toddalia* or related genera. This raises the question of why agromyzid leaf miners adapted to feeding on these plants before or during the Paleogene, but this trait did not persist or recur in any recent lineages. Answers to this question must necessarily be speculative, but the extensive fossil history of Platanaceae, including traces of other extinct herbivore associations, may be relevant. Although now a species-poor, minor element of temperate and arid subtropical climates, Platanaceae was a relatively diverse and important component of middle Cretaceous to Paleogene floras at middle latitudes (Manchester, 1986; Crane et al., 1988; Graham, 1999; Johnson and Ellis, 2002). Other analogous examples of extinct herbivore associations with Platanaceae are known, including borings of the cambium-mining agromyzid *Palaeophytobia platani* Süss and Müller Stoll, 1975. In addition, the North American, extinct platanaceous genus *Macginitiea* Wolfe and Wehr, 1987 (see also Manchester, 1986) harbored distinctive leaf mines of Incurvariidae (Lepidoptera) similar to extant *Paraclemensia* Busck, 1904 (Labandeira, 1998b), species of which no longer mine Platanaceae but do consume several unrelated genera, particularly species of *Acer* L. (Sapindaceae) in North America.

The traditional view of adaptive radiation in phytophagous insects (e.g., Ehrlich and Raven, 1964) emphasizes the filling of niches (i.e., host plant species) by insect lineages following infrequent colonization events of novel plant clades. Following such episodes of adaptive radiation, associations are presumably often stable over long geologic periods, as has been noted for many insect groups (Wilf et al., 2000; Winkler et al., 2008), unless replaced by subsequent radiations of other insect lineages on the same host. Under this paradigm, ancient or relictual host associations should be common in the recent fauna and, indeed, many known examples exist (Wilf et al., 2000; Winkler et al., 2008). Much more rare in the literature, and more difficult to document, are cases like the present ones of extinct host associations, despite the continued presence of closely related hosts and herbivores. If found to be more frequent, such cases will suggest a more complex evolution of plant-insect associations, in which extinction of lineages and associations may play a major role.

Although most agromyzid species today specialize on herbaceous hosts, it is possible that woody plants were more important in the early evolution of Agromyzidae. For instance, *Agromyza*, the earliest branching genus in the subfamily Agromyzinae (Scheffer et al., 2007), has at least 16 morphologically diverse species that feed on woody hosts in six different families. In contrast, in the genus *Phytomyza*, most species feeding on woody plants belong to a single, relatively recent lineage that shows a much higher incidence of host family shifts than other *Phytomyza* lineages (Winkler et al., 2009a). This pattern of elevated host-shift frequency in woody plant specialists probably holds true across other insect groups as well (Feeny, 1975), suggesting that early agromyzid radiations on woody hosts may have colonized more taxa than are presently observed as host plants. Alternatively, an early radiation of agromyzid taxa on herbaceous hosts may have occurred but is not recorded in the known fossil record, because deposits with abundantly preserved nonwoody plants are uncommon and rarely dominate local habitats (but see Wing et al., 1993; Johnson, 2002 for some latest Cretaceous examples). Because of preservational bias toward woody taxa,

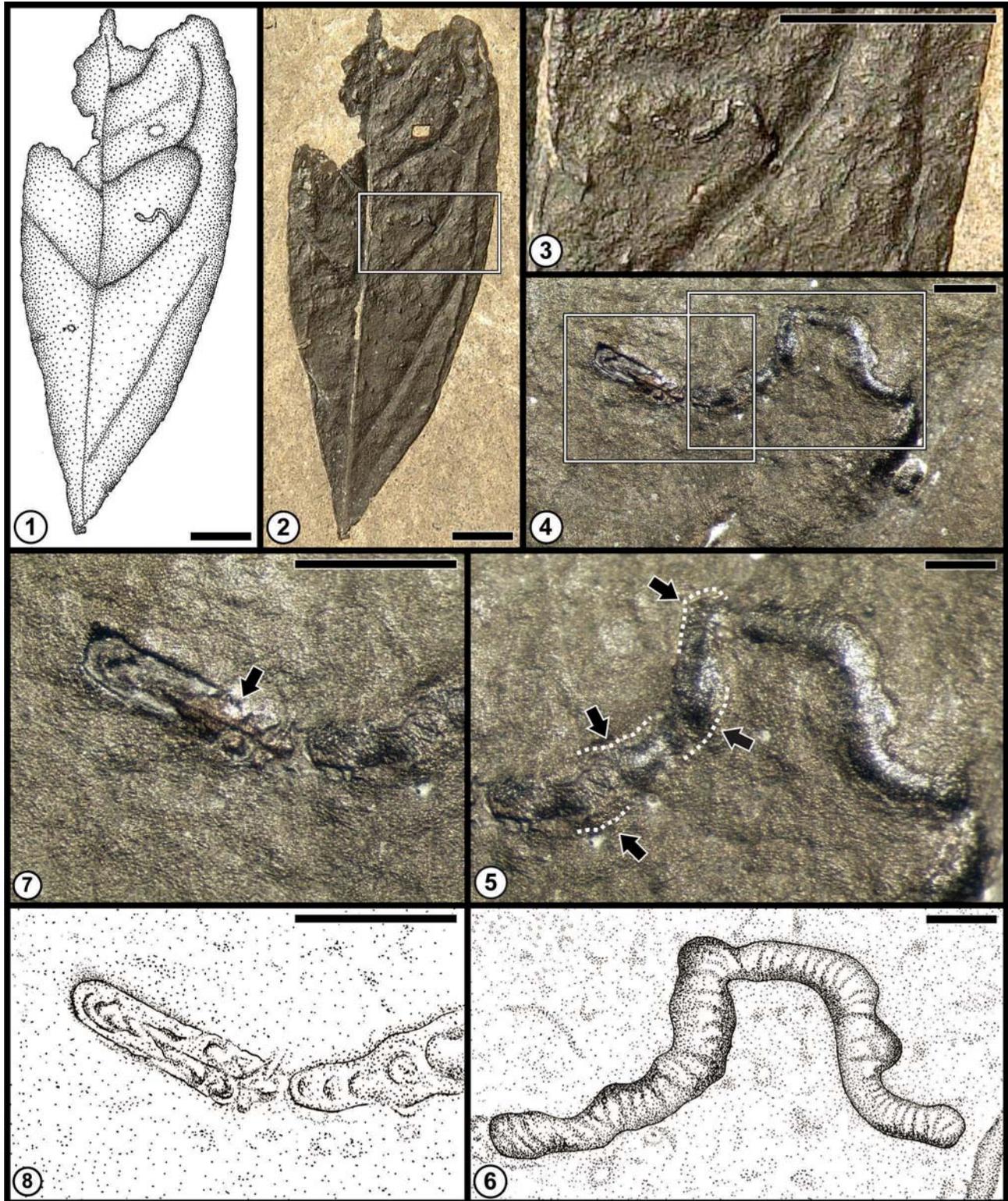


FIGURE 8—1-8, *Phytozites schaaerschmidti* nov. ichnosp., holotype (specimen SM.B Me 822), from Eocene of Messel, in Germany, on *Toddalia ovata* Wilde, 1989 (Rutaceae). 1, an overlay drawing of the entire leaf specimen, showing the location of the mine; 2, photograph of leaf specimen depicted in 1, showing area magnified in 3-6 below; 3, a close-up of the complete mine, originating on a secondary vein; 4, detail of mine with fluidized frass trail; 5, segment from middle portion of mine, showing laterally positioned, alternating frass bands (black arrows, with dotted lines external to frass bands) characteristic of agromyzid leaf-miners; 6, drawing of area pictured in 5, showing alternating frass bands; 7, close-up of terminal portion with possible larval or puparial remains (black arrow); 8, drawing of area pictured in 7. Scale bars: 1-3 = 5 mm; 4-8 = 1 mm.

a missing record of colonization, especially on more basal herbaceous angiosperms, may be attributable to sampling issues rather than any intrinsic biological pattern. One should note that at least some radiations of agromyzid species on herbs such as grasses (Poaceae) and composites (Asteraceae) appear to truly reflect mid-Cenozoic events, associated with major diversification and expansion of these herbaceous lineages during the Oligocene and Miocene (Niklas et al., 1985; Strömberg, 2005; Barreda and Palezzesi, 2007; Winkler et al., 2009b).

Wilf et al. (2006) noted that the type locality of *Phyto-myzites biliapchaensis*, Mexican Hat, is characterized by an extremely diverse herbivore trace fauna feeding on a low-diversity flora. Although locally abundant at this site, agromyzid traces were not found at any other of the few hundred Late Cretaceous and Paleocene sites studied by these authors (Labandeira et al., 2002a, 2002b; Wilf et al., 2006), among several thousand fossil leaves of Platanaceae that were examined. It was suggested that the Mexican Hat locality and other early Paleocene North American sites represent ecosystems with unbalanced food webs still recovering from the end-Cretaceous mass extinction approximately 1 Ma earlier, during which many insect herbivores went extinct (Labandeira et al., 2002a, 2002b, Wilf et al., 2006). As the most specialized of the major feeding types, the fauna of leaf-mining and galling herbivores were found to be especially affected by this event, including those on Platanaceae (Labandeira et al., 2002b). Although the ecologically destabilizing extirpation of plant-insect associations seen at the end-Cretaceous in Western North America may not have been globally uniform (Wappler et al., 2009), it is possible that the origin and early evolution of Agromyzidae may be closely tied to the end-Cretaceous event. The early Paleocene interval of unbalanced food webs and changing climate and floral composition probably provided an opportunity for the ecological and evolutionary expansion of the Agromyzidae. We hope this report will encourage discovery and accurate determination of additional early Cenozoic leaf-mine material in order to better document the evolution of Agromyzidae and other leaf-mining taxa during this critical period.

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