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New leaf-mine fossil from the Geumgwangdong Formation, Pohang Basin, South Korea, associates pygmy moths (Lepidoptera, Nepticulidae) with beech trees (Fagaceae, *Fagus*) in the Miocene

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Abstract.—A nepticulid leaf-mine ichnofossil, *Stigmellites janggi* Sohn and Nam, n. ichnosp., is described on the basis of a fossil leaf of *Fagus* from the early Miocene Geumgwangdong Formation in Pohang Basin. This mine trace is characterized by a linear-blotch type with a clear centric frass trail composed of closely and randomly dispersed pellets filling the mine width in the early stage. We found traces of a possible egg case and an exit slit from the leaf. These features are most consistent with those produced by members of Nepticulidae. Our record demonstrates for the first time the trophic association of Nepticulidae with *Fagus* in the Miocene and suggests the persistence of a long-term association between the insect family and the plant genus from the Miocene to the present. Other Nepticulidae leaf mines in the Miocene and leaf-mine fossils from the Geumgwangdong Formation are briefly reviewed.

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Introduction

The Lepidopteran fossil record is notoriously incomplete because of its paucity and biases (Kapoor, 1981; Kristensen and Skalski, 1999; Sohn et al., 2015). The body fossils of microlepidopterans assignable to a family level with relevant evidence are critically scarce (Sohn et al., 2015; de Jong, 2017). In such cases, their characteristic feeding damage, e.g., leaf mines preserved on fossilized host plants, acts as an important supplement. Moreover, such fossils provide direct evidence of the interactions between lepidopterans and plants (Labandeira et al., 1994; Lopez-Vaamonde et al., 2006; Donovan et al., 2014).

Nepticulidae is one of the major leaf-mining insect groups, currently including 22 genera and 862 species worldwide (van Nieukerken et al., 2016). The adult moths are the smallest in Lepidoptera, hence are commonly known as pygmy moths, and represent some of the earliest diverging lineages in lepidopteran phylogeny (Regier et al., 2015). The larvae exhibit various forms of endophagous herbivory, of which the majority are leaf miners. The larval host plants are primarily dicotyledonous, arboreal angiosperms, although some lineages are associated with monocotyledons or herbaceous hosts (Davis, 1999). Nepticulidae could have been among the first lepidopteran groups to start using angiosperms (Doorenweerd et al., 2016). Currently, there are 79 records of nepticulid fossils, as both body and trace fossils, known in the world (Sohn et al., 2012; Doorenweerd et al., 2015). The earliest confirmed fossil occurrence of Nepticulidae was 102 million years ago; since then, there has been a fairly regular occurrence of such mines in the fossil record (Labandeira et al., 1994; Doorenweerd et al., 2015).

In their review, Doorenweerd et al. (2015) described the diagnostic features of nepticulid leaf mines as: (1) the presence of an egg-case or its trace involving the oviposition by a female at the beginning of the leaf mine, although this can be secondarily lost; (2) the path of the leaf mine varying species by species, but often limited by the midvein or other prominent veins on a leaf; (3) the patterns of frass deposition variable, but a frass trail in meniscate arcs is exclusively seen in some nepticulid leaf mines; and (4) the presence of a semicircular slit representing the exit hole for pupation near the end of the leaf mine.

This study describes a leaf-mine fossil from the early Miocene Geumgwangdong Formation in Pohang Basin, South Korea, identifies the mine-maker (Nepticulidae), and reviews the occurrence of the nepticulid leaf mines in the Miocene.

Geological setting

Stratigraphic information.—The fossil specimen in this study was discovered from the Geumgwangdong Formation in Pohang City, Republic of Korea (Fig. 1.1). This formation belongs to the Janggi Group, which is a representative fossil bed for Neogene plant leaves on the Korean Peninsula (Yoon, 2010). The paleoflora of the Janggi Group are comparable to the Aniai-type flora typified by cool-temperate vegetation during the early Miocene (Huzioka, 1972). Coinciding with this, Ar-Ar dating estimated the age of the rocks in the Janggi Basin as belonging to the early Miocene, ca. 21.5–14.6 Ma (Paik et al., 2010). The Geumgwangdong Formation (Figs. 1.2, 1.3) is ~70 m thick and dominated by lacustrine deposits consisting of paper shale, shaly mudstone, laminated silty mudstone, and mudstone (Paik et al., 2012).

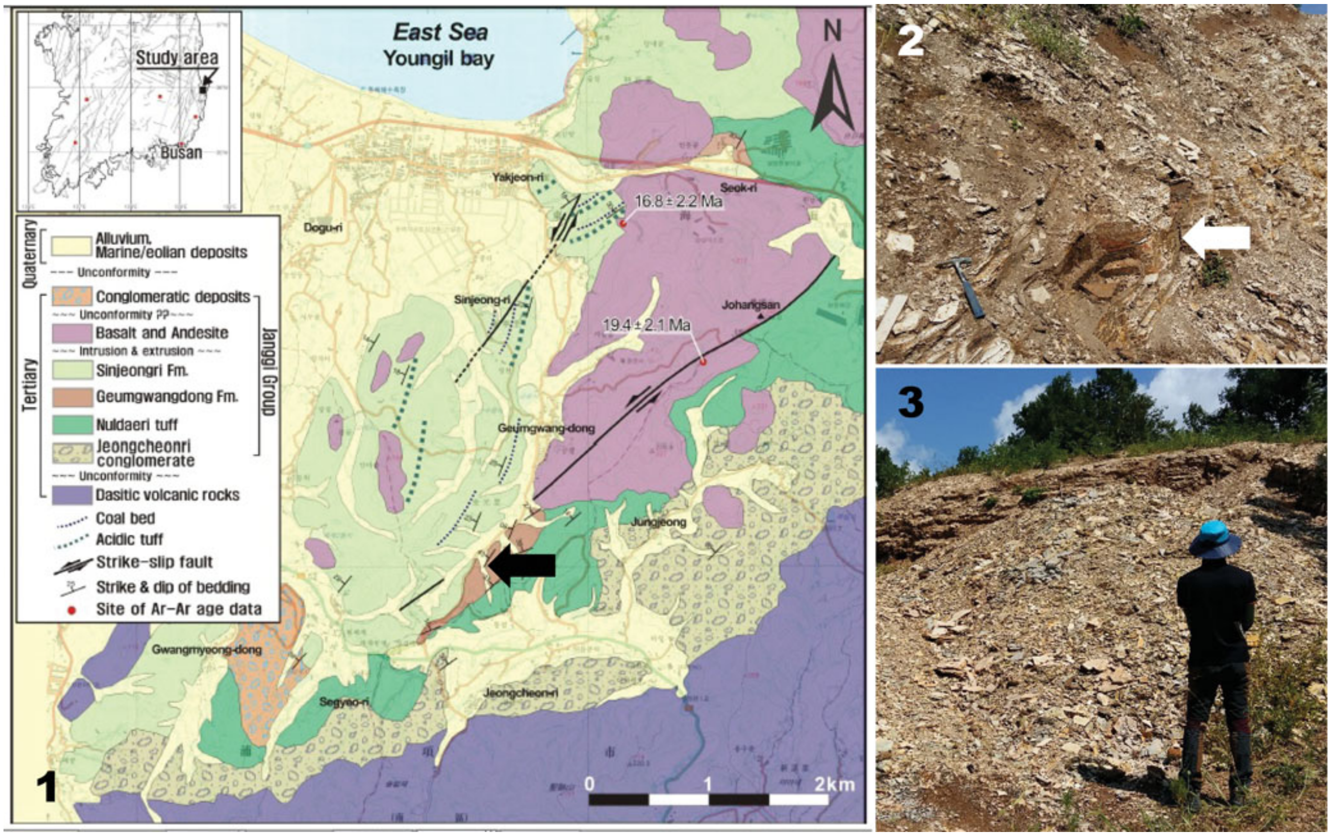

Figure 1. Maps and photographs of the study area: (**1**) geological map of Pohang Basin (after Paik et al., 2012), with black arrow indicating study area; (**2**) fossil locality along a mountain slope, with arrow pointing to fossiliferous horizon; (**3**) a pile of paper shales taken off the mother beds nearby.

Paleobiota.—The Geungwangdong Formation has yielded a large number of the compression/impression fossils of leaves and fruits of various plant species (Kanehara, 1936; Huzioka, 1972; Chun, 1982; Kim and Choi, 2008; Jeong et al., 2010). Paik et al. (2012) listed 64 taxa of fossil plants belonging to 27 families and 43 genera in the formation. The dominant groups included *Fagus* Linnaeus, 1753, *Quercus* Linnaeus, 1753 (Fagaceae), *Betula* Linnaeus, 1753 (Betulaceae), *Zelkova* Spach, 1841 (Ulmaceae), *Acer* Linnaeus, 1753 (Sapindaceae), Leguminosae, and *Metasequoia* Hu and Cheng, 1948 (Cupressaceae), which represented tall tree vegetation from mountain slopes and valleys (Paik et al., 2010). In coincidence with this, Mollusca and Estheria, two groups commonly occurring in freshwater lake sediments, have not been found in the formation (Paik et al., 2010). Several animal remains have been discovered from the Geumgwangdong Formation (unpublished data, K-S Nam). However, only a few of these, including fish bones (Yoon, 1992) and insects (Kim and Lee, 1975; Kim, 1976), have been studied.

Materials and methods

Observation.—The fossil leaf was examined using a stereomicroscope (Leica EZ4) and photographed using a digital camera (Nikon D40) in a general light box or with an adapter connected to a dissecting microscope (Leica MZ6).

Terminology.—Terms for leaf and leaf-mine morphologies follow Ellis et al. (2009) and Hering (1951), respectively. Sequential numbers of the secondary (2°) veins in the leaf were counted successively from the most basal vein.

Repository and institutional abbreviation.—The type specimen examined in this study is deposited in the collection of the Daejeon Science High School for the Gifted, Daejeon, South Korea (DSHS).

Systematic paleontology

Order Lepidoptera Linnaeus, 1758
Suborder Glossata Fabricius, 1775
Superfamily Nepticuloidea Stainton, 1854
Family Nepticulidae Stainton, 1854
Genus *Stigmellites* Kernbach, 1967

1967 *Stigmellites* Kernbach, p. 104.

Type species.—*Stigmellites heringi* Kernbach, 1967.

Remarks.—*Stigmellites* was originally established as an ichnogenus but later changed to a collective-group name (for a full history, see Sohn and Lamas, 2013). According to this change, *Stigmellites* included the nepticulid fossils for which a generic association could not be determined due to lack of

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evidence. Robledo et al. (2016) rejected such a change and amended the diagnoses of *Stigmellites* based on only mine morphologies, not references to trace makers. We prefer to use *Stigmellites* as a collective-group name in two reasons. First, such usage retains information on taxonomic affinities of trace fossils, often more important than their morphological features. Bertling et al. (2006, p. 279; also cited by Robledo et al., 2016), in fact, argued that producer-based ichnotaxon names are inappropriate, when the assignments are ambiguous. The ichnogenus *Stigmellites* includes trace fossils whose producers are reliably identifiable at the family level (Doorenweerd et al., 2015). Secondly, the amendment of *Stigmellites* by Robledo et al. (2016) necessitates several nomenclatural changes, including designation of many singleton morphotaxa and a new collective-group name. We do not find such actions more advantageous than simply retaining *Stigmellites* as a collective-genus name. *Stigmellites* currently comprises one adult moth in amber and 16 species based on trace fossils, spanning the Late Cretaceous to the late Pliocene (Doorenweerd et al., 2015).

Stigmellites janggii Sohn and Nam, new ichnospecies
Figures 2.1, 2.3, 3

Holotype.—DSHS-2017201 (only original part present).

Diagnosis.—This ichnospecies differs from the late Pliocene *Stigmellites pliotityrella* Kernbach, 1967 associated with *Fagus sylvatica* Linnaeus, 1753 in Germany in having a serpentine mine path (rather straight in *S. pliotityrella*) and a clear centric frass trail. Among the Miocene nepticulid fossils, *S. janggi* n. ichnosp. is similar to a nepticulid leaf mine on *Quercus virginiana* Miller, 1768, found in the USA (Opler, 1973), but differs from the latter in having a narrower and longer mine path.

Description.—The mine trace (Fig. 2.3) commences near the distal one-fifth of the fifth 2° vein and proceeds between the third and the seventh 2° veins, roughly toward the midvein. There is a small, elliptical void possibly corresponding to a lost egg case. From the starting point, the mine runs toward the fourth 2° vein for a short distance, recurves, continues beyond the fifth 2° vein, recurves again near the sixth 2° vein, keeps running in slightly sinuous way, approaches the leaf margin at the fourth 2° vein, and then turns toward the third 2° vein. There, the mine runs along the third 2° vein toward the midvein, serpentines between the third and fourth 2° veins, and then runs along the fourth 2° vein toward the midvein for a moderate distance. After that, the mine obliquely proceeds beyond the fifth 2° vein, reaches the branching point of the midvein and the sixth 2° vein, and then runs along the basal two-fifths of the sixth 2° vein. Immediately after crossing the sixth 2° vein, the mine becomes an elliptical blotch parallel to the sixth 2° vein, enlarged toward the midvein. The frass trail starts in the beginning of the mine and ends before the blotch part of the mine. The frass patterns are present as a central line of randomly-distributed pellets, gradually broadening as the mine proceeds. The frass trail fills the width of the mine in the proximal third and takes up half of the mine width in the distal two-thirds. In the blotch part of the mine, the frass granules are irregularly aligned along the circumference. A semicircular slit is present near a branch of the midvein and the sixth 2° vein.

Etymology.—This ichnospecies is named after the sediment where the fossil was discovered.

Classification.—This mine can be classified as a full-depth, partially serpentine, linear-blotch leaf mine. In the morphotyping system by Labandeira et al. (2007), *Stigmellites janggii* n. ichnosp. could fall into DT90 (DT = damage type) but differs from the latter in having a more sinuous mine path and a continuous frass trail.

Modern analogs.—Among the extant species of Nepticulidae feeding on *Fagus*, the fossil leaf mine is similar to those (Fig. 2.2) made by a European species, *Stigmella hemargyrella* (Kollar, 1832), but differs from the latter in having a less-dispersed frass trail and in lacking the frass pattern in meniscate arcs. There is also an undescribed species of *Stigmella* that feeds on *Fagus* in Taiwan, and undescribed species of *Stigmella* and *Ectoedemia* Busck, 1907 in Japan that feed on *Fagus* and produce similar leaf mines (unpublished data, C. Doorenweerd). The leaf-mine type is not very distinctive and various other modern analog species feeding on deciduous woody plants could be indicated.

Preservation.—The whole block is a pale brown, subtriangular shaly mudstone, 17.8 cm in maximum length, 17 cm in maximum width, and ~ 5 cm in maximum thickness. The fossil leaf (Fig. 2.1) is a compression situated on a margin of the block with its apical quarter taken off. Parts of teeth and petiole have been preserved in the specimen. The face opposite the leaf mine bears three plant fragments: two monocotyledonous leaves and one dicotyledonous leaf.

Measurements.—The total length of the linear mine is ~ 140 mm; the mine path is limited to a space of 24 mm x 21 mm; path lengths between turning points range 3–10 mm; the blotch-mine section is 9.5 mm in length and 3–5 mm in width; the leaf after reconstruction is ~ 850 mm in length and ~ 45 mm in maximum width.

Host plants.—This fossil leaf can be assigned to *Fagus* (Fagaceae) based on a diagnostic combination of three characteristics of the genus (Leng, 1999; Manchester and Dillhoff, 2004; Xu et al., 2016): the absence of spines on the teeth, the lack of fimbrial veins, and the presence of fagoid teeth. It also shares the common features of *Fagus*, including short petioles, lamina with evenly spaced, parallel secondary veins and closely spaced percurrent tertiary veins, the lack of intersecondary and pectinal veins, and a serrate margin with nonglabular teeth arranged one per secondary vein (Manchester and Dillhoff, 2004). *Fagus antipofi* Heer, 1858 has been recorded from the Geumgwangdong Formation (Paik et al., 2012). The overall shape of the fossil leaf on our specimen is consistent with those of the small leaves of *F. antipofi*, illustrated by Tanai (1961).

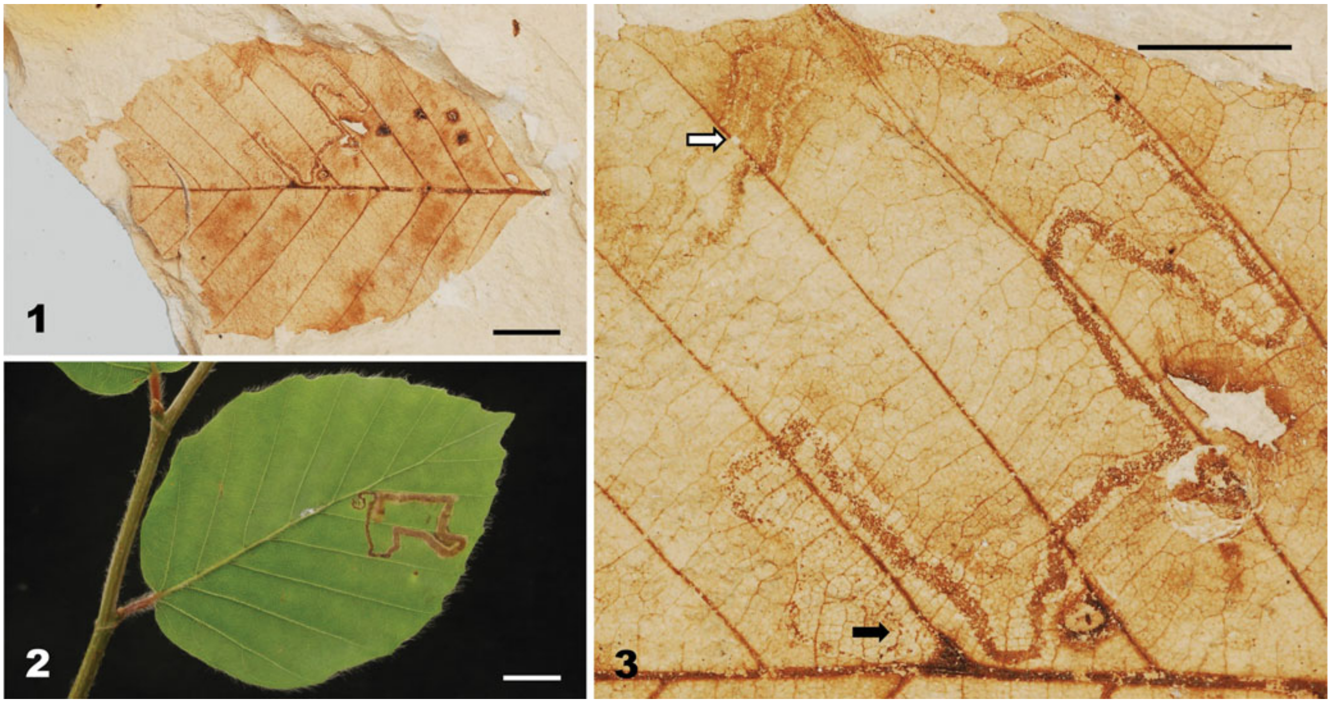

Figure 2. Photographs of leaf mines: (**1**) a whole leaf fossil of *Fagus antipofi* with leaf-mine trace (holotype of *Stigmellites janggii* n. ichnosp., DSHS-2017201); (**2**) a leaf mine of the extant nepticulid, *Stigmella hemargyrella* on *Fagus sylvatica* (photo by György Csóka); (**3**) detail of Figure 2.1, with white and black arrows indicating traces of an egg case and an exit slit, respectively. Scale bars = 10 mm (**1, 2**), 5 mm (**3**).

Remarks.—Association of this fossil with Nepticulidae is substantiated by a combination of similarities with extant nepticulid leaf-mines: (1) a narrow linear mine path not crossing a primary vein; (2) the presence of traces possibly corresponding to an egg case and an exit slit; and (3) a frass trail filling the width of the mine in the early phase and not greatly broadening along the mine path. Based on the host plant and the shape of the mine, the mine maker could belong to the large extant genus *Stigmella* Schrank, 1802. However, linear-blotch mines are common among nepticulid genera and

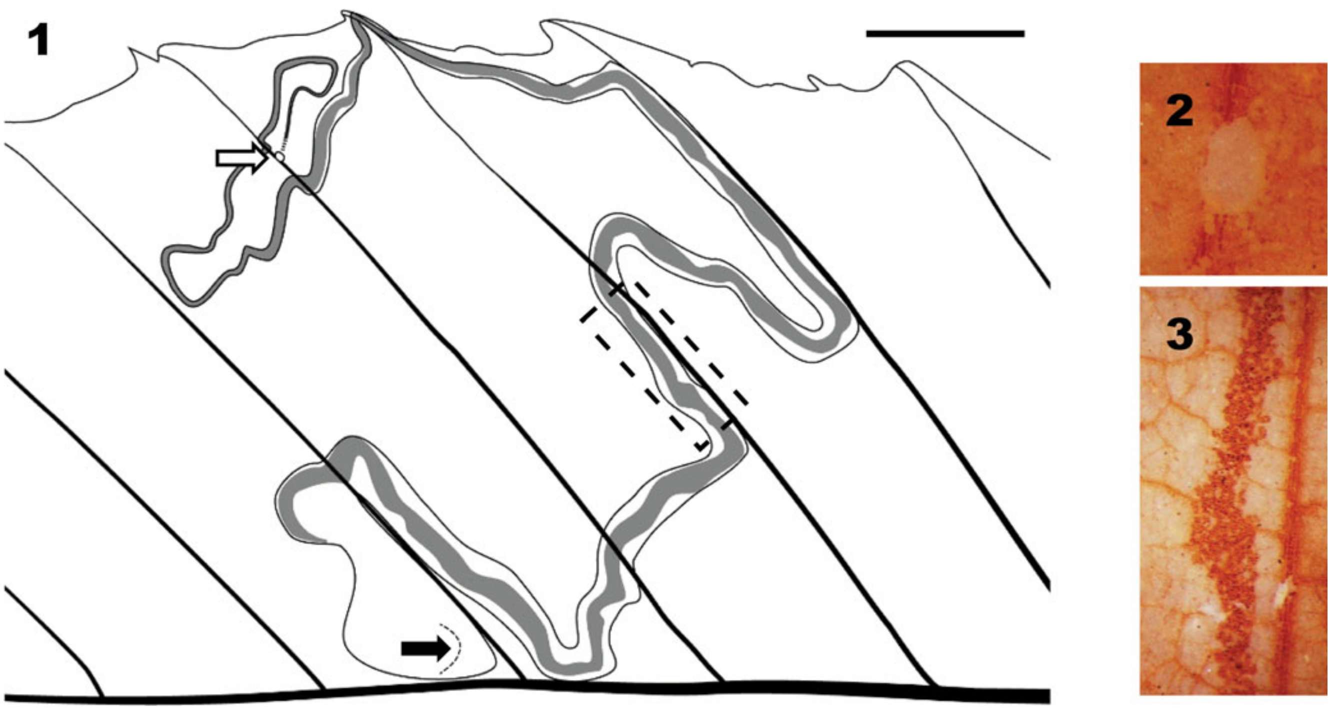

Figure 3. Drawing and photographs of *Stigmellites janggii* n. ichnosp.: (**1**) line drawing of the leaf mine in Figure 2.3, with gray area indicating a frass trail, and white and black arrows indicating traces of an egg case and an exit slit, respectively; (**2**) detail of a void corresponding to an egg case (white arrow in Fig. 3.1); (**3**) detail of a part of the frass trail corresponding to dashed box in Figure 3.1. Scale bar = 5 mm.

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our knowledge of *Fagus*-feeding nepticulids is very limited. Although most nepticulid species are conservative to the plant family they feed on, there are exceptions and common plants are used by multiple genera (Doorenweerd et al., 2015). Thus, assignment of this fossil to the genus *Stigmella* is pending.

Discussion

The Miocene fossils of nepticulid leaf mines have been found in several sediments worldwide covering the entire epoch. The host plants for these fossils include Berberidaceae (Liebhold et al., 1982), Betulaceae (Kuroko, 1987), Fagaceae (Opler, 1973), Lauraceae (Peñalver, 1997), Schisandraceae (Knor et al., 2012) and Symplocaceae (Martins-Neto, 1989). In Fagaceae, Miocene leaf mines of nepticulids have previously been found exclusively associated with *Quercus* leaves (Opler, 1973), whereas none were known on beeches (*Fagus*). The earliest and only nepticulid leaf-mine fossil on beeches is from the Pliocene (Kernbach, 1967). Paik et al. (2012) recorded a leaf-mine fossil on *Fagus* from the Geumgwangdong Formation (early Miocene), but did not identify the mine maker. Therefore, *Stigmellites janggi* n. ichnosp. is the first confirmed nepticulid leaf mine associated with the fossil leaves of *Fagus* in the Miocene.

Beech trees are one of the representative components of temperate deciduous broad-leaf forests of the Northern Hemisphere (Denk, 2003). They generally occupy a climatic space spanning cool temperate and warm temperate zones (Fang and Lechowicz, 2006). Leaves of *Fagus* have been found in large numbers in the early Miocene Geumgwangdong Formation (Paik et al., 2010, 2012). The paleoflora of this formation has been compared to the Aniai-type flora in Japan, which indicates cool-temperate vegetation. Paik et al. (2012) examined 83 fossil leaves of *Fagus* from the Geumgwangdong Formation and found that ~ 60% was damaged by insects. Among the insect damage types, external feeding was responsible for the greatest proportion, whereas mining was only responsible for 3% of the total damaged leaves.

This is the first study to identify the makers of the leaf-mine fossils from the Geumgwangdong Formation. Paik et al. (2012) illustrated two exemplar leaf-mine fossils, one on *Fagus* and the other on *Ulmus* Linnaeus, 1753. Both leaf mines appeared to have a nepticulid origin. The mine trace on the fossil *Fagus* leaf exhibited a serpentine path with a centric frass trail that enlarged as it proceeded. The mine path was limited to between the secondary veins, indicating that the maker was very small, as are nepticulids. The mine fossil on *Ulmus* exhibited frass patterns in meniscate arcs that are often observed in nepticulid mines. *Stigmellites janggi* n. ichnosp. is distinguished from those two leaf mines in the shapes of mine path and frass trail and in the presence of the terminal blotch phase, indicating a different species of Nepticulidae was involved. Herbivorous insect fauna from the Geumgwangdong Formation has not been thoroughly investigated to date. There was a jewel beetle (Buprestidae) recorded from the formation (Kim, 1976), but no lepidopterans.

Extant Nepticulidae feeding on *Fagus* also appears to be little studied, with undescribed species known from Taiwan and Japan (unpublished data, C. Doorenweerd). There are two commonly observed species of *Stigmella* in Europe that feed on *Fagus sylvatica*: *S. hemargyrella* and *S. tityrella* (Stainton, 1854) (Ellis et al., 2018). The latter produces leaf mines similar to the Pliocene species, *Stigmellitis pliotytirella*, which was found in Germany (Kernbach, 1967). Apart from *Stigmella*, only *Ectoedemia* species are currently found feeding on *Fagus*. Both *Stigmella* and *Ectoedemia* are diverse on oaks (*Quercus*), both in extant and fossil fauna (Doorenweerd et al., 2015, 2016). It is noteworthy that leaf-mine examples on *Fagus* from the Geumgwangdong Formation indicate two nepticulid associations on the same fossil plant species. Because *Fagus* trees were a more dominant part of forests in Neogene Asia than in present day (Peters, 1997), it is likely that there was a more diverse fauna of leaf miners associated with beeches than there is today.

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