

Biology of a leaf miner (Coleoptera) on *Liaoningocladus boii* (Coniferales) from the Early Cretaceous of northeastern China and the leaf-mining biology of possible insect culprit clades

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Abstract

Specimens of the broad-leaved conifer, *Liaoningocladus boii* Sun, Zheng & Mei 2000 were evaluated from the mid Early Cretaceous Yixian Formation occurring overwhelmingly at Dawangzhangzi, Liaoning Province, NE China. Arthropod-mediated plant damage types (DTs) were categorized for 343 specimens of this host; one of these DTs represented a distinctive leaf-mine, DT280, established as *Fossafolia offae* Ding, Labandeira & Ren, *ichnogen. et ichnosp. nov.* A comparison of DT280 to analogous modern leaf mines was based on: (1) leaf-mine features observed in modern leaf mines; (2) likelihood of a particular leaf-mine culprit lineage being present, given phylogenetic evidence; and (3) body fossils of the candidate culprit occurring in the same or a spatiotemporally proximal deposit. Evidence from these three and other sources of information indicate the most likely miner of *F. offae* was an extinct species of Buprestidae (Coleoptera), perhaps similar to modern leaf-mining tribe Trachyini. Much less likely affiliations were Mordellidae, Chrysomelidae and Curculionioidea. *Fossafolia offae* leaf mines were produced by a larva that consisted of four instars, engaged in full-depth tissue feeding, partitioned into a linear, earlier-phase mine with a distinctive frass trail and a more blotch-like, later-phase mine. Adults of this leaf miner likely fed on *L. boii*, producing linear patches of intercostal window feeding, assigned to DT103, or less likely, may have been a pollinator. The adult female likely laid eggs singly into leaf tissues between adjacent major veins, resulting in DT101 ovipositional damage. This study provides for the use of multiple damage-types to document life-history feeding traits for a single herbivore species. Consequently, we introduce the *damage-type suite* concept to refer to two or more different damage types genetically linked to the same culprit herbivore that issue from different developmental stages (larvae, adult), or are produced by different tissue-penetrating insect organs (ovipositors, mouthparts). In addition, we provide a basis for using three types of general evidence necessary to elucidate identification of the culprit.

Key words

Buprestidae, conifer, damage-type suite, Dawangzhangzi, external foliage feeding, *Fossafolia*, host-specialist, leaf mining, oviposition.

1. Introduction

Plant-insect associations attract great interest from biologists and paleobiologists because of the ecological information they provide, including the potential for documenting associations among organisms during long stretches of geological time (LABANDEIRA 2002). One par-

ticular association, leaf-mining, is of special interest as it is ideally suited to document intimate and specialized interactions between an insect and its plant host. Leaf miners possess feeding habits different to those of more familiar external foliage feeders by inhabiting the same

tissue that is being consumed. Consequently, leaf miners consume live foliage from within, either of a single tissue stratum, such as epidermis, or multiple tissue layers that would include, for example, palisade parenchyma and spongy mesophyll (NEEDHAM et al. 1928). Unlike galls, leaf miners do not elicit abnormal host-tissue response other than occasionally a thin lining of callus along late-phase mine edges (HERING 1951). Along with galls and perhaps seed predators, leaf miners are among the most highly specialized of herbivorous insects, and numerous mining lineages have developed intricate associations with their host-plants (NEEDHAM et al. 1928; CONNOR & TAVERNER 1997; LOPEZ-VAAMONDE et al. 2006; WHITEMAN et al. 2011). Leaf-mining only occurs in the four, highly diverse holometabolous orders of: (1) Hymenoptera, where leaf mining occurs in three families (SMITH 1993); (2) Lepidoptera, involving 34 families (POWELL et al. 1998); (3) Diptera, present in 18 families (LABANDEIRA 2005); and (4) Coleoptera, with eight leaf-mining families (GREBENNIKOV 2013).

Although several fossil occurrences from the late Paleozoic once were considered examples of leaf mining, currently there is no convincing evidence for such attribution (LABANDEIRA 1998a, 2006a). The earliest credible leaf-mining fossil records have been reported from Kyrgyzstan, Austria, Australia and South Africa in deposits of mid-Triassic age (TILLYARD 1922; ROZEFELDS & SOBBE 1987; KRASSILOV & KARASEV 2008; ZHERIKHIN 2002; SCOTT et al. 2004; LABANDEIRA & ANDERSON 2005; LABANDEIRA 2006a; MELLER et al. 2011). Globally, these Triassic leaf mines occurred on several plant lineages that included ferns, sphenophytes and a broad repertoire of seed plants, such as cycads, seed ferns, broad-leaved conifers, and ginkgophytes. These hosts were colonized by a variety of leaf miners, best demonstrated in the Molteno Flora of South Africa (SCOTT et al. 2004; LABANDEIRA 2006a). Leaf-mined plants have a poor record in Jurassic deposits (ROZEFELDS 1988; SCOTT et al. 1992; LABANDEIRA 1998b; ZHERIKHIN 2002), but more abundant occurrences are found in Cretaceous deposits (KOZLOV 1988; LABANDEIRA et al. 1994).

The character of the leaf-mine record improves marginally during and after the diversification of angiosperms in the mid Cretaceous. A latest Early Cretaceous deposit, the Dakota Formation of midcontinental U.S.A., has yielded several early angiosperm plant taxa that bore a variety of mine types attributed to Lepidoptera (STEPHENSON 1991; SCOTT et al. 1992; LABANDEIRA et al. 1994). Other mid-Cretaceous leaf mines that targeted mostly angiosperms were reported by FRITSCH (1882), KNOWLTON (1917), KOZLOV (1988), KRASSILOV (2007, 2008), and KRASSILOV & BACCHIA (2000). At the Late Cretaceous-Paleogene interval, during a later phase of angiosperm diversification, numerous modern lineages of leaf-mining insects enter the record, based on body fossils (SOHN et al. 2012) and insect damage (STEPHENSON & SCOTT 1992; LANG et al. 1995; LABANDEIRA 1998c; SOHN et al. 2012), most of which were Lepidoptera. During the early Paleogene Period, the earliest dipteran leaf mines have

been attributed to Agromyzidae (WINKLER et al. 2010). Rare leaf mines representing other groups of insects, including Coleoptera, also have been reported (STEPHENSON 1991; LANG et al. 1995; LABANDEIRA 1998c). During the subsequent Neogene Period, leaf mines attributed to the four leaf-mining insect orders become more diverse and abundant (STRAUS 1977; GIVULESCU 1984). Despite this record, the autecology of leaf-mining insects throughout the Mesozoic and Cenozoic remains largely unknown.

Given the sparse, Mesozoic leaf-mine record, it is notable that a new and distinctive Early Cretaceous (late Barremian) leaf mine occurs on *Liaoningocladus boii* Sun, Zheng & Mei 2000, from the Yixian Formation of northeastern China. *L. boii* is a broad-leaved conifer established by SUN et al. (2000), but of uncertain family-level affinities. The distinctive ovulate organs, foliar cuticular structure and taxonomic affiliation of *L. boii* is being examined (G. Sun et al. pers. comm.), although currently *L. boii* is not assigned to a particular clade within the Coniferales. As the most abundant plant at the Dawangzhangzi locality of northeastern China, *L. boii* harbors a distinctive component community (ROOT 1973) of insect and mite herbivores. This is the first report that identifies and places in a broader ecological and evolutionary context the plant-insect associations of *L. boii*.

In this study, a unique leaf-mining damage type, DT280, is described that occurs on host *L. boii*. We discuss two additional host-associated damage types, DT101 (oviposition) and DT103 (surface feeding), which often are associated with the leaf mines. The concept of the *damage-type suite* is introduced to consist of a set of damage types that was made by the same insect herbivore species based on feeding by different life stages (larval instars, adult) or from different damage types through organs of contact with the plant surface (ovipositor, mouthparts). The damage-type suite is a hypothesis that provides important life-history data for a single, herbivorous arthropod species that can be tested by other occurrences on the same or similar hosts in the deep past. Establishment of the damage-type suite necessarily involves, the identity of the leaf-mining culprit, an important theme of this report, which is inferred by three lines of evidence that taxonomically circumscribes the taxon responsible for the *L. boii* leaf mine.

2. Geologic and biologic setting

All 343 *Liaoningocladus boii* specimens were collected near Dawangzhangzi Village in Liaoning Province of northeastern China (Fig. 1; 41°08'02"N 119°15'45"E). This site occurs within the Yixian Formation and has been radioisotopically dated as mid Early Cretaceous (late Barremian), at ca. 125 Ma [= million years ago] (SWISHER et al. 1999; ZHOU et al. 2003). The Yixian For-

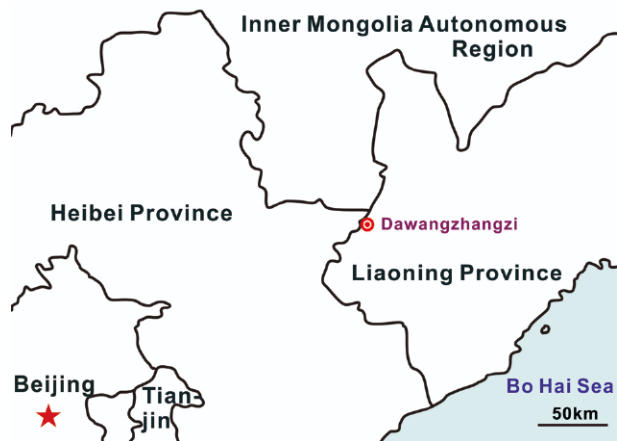


Fig. 1. The fossil site of Dawangzhangzi is located near the junction of the Inner Mongolia Autonomous Region and Hebei and Liaoning Provinces, in northeastern China.

mation was formed by a cycle of volcanic eruptions and associated sedimentation. The sediments of the Yixian Formation are lacustrine in origin, intercalated with volcanic rocks (REN et al. 1995). Jehol Group strata, which include the Yixian Formation, represent freshwater lacustrine environments, and lack the laterally variable sedimentary facies of other freshwater settings such as rivers and deltas (ZHOU et al. 2003). The excellent and frequently complete or near-complete preservation of fossils, particularly plants, arthropods and vertebrates, indicates that all Yixian sites originated in proximity to low-energy deposits of a large lake and were not transported over extensive distances (ZHOU et al. 2003).

Dawangzhangzi is a locality typical of the Jehol Biota that yields numerous, excellently preserved animal and plant fossil taxa. Important Dawangzhangzi taxa include the fish *Lycoptera davidi*, the reptile *Hyphalosaururus lingyuanensis*, the bird *Liaoxiornis delicatus*, the mammal *Eomaia scansoria*, and the early angiosperm *Archaeofructus sinensis* (SAUVAGE 1880; GAO et al. 1999; HOU & CHEN 1999; JI et al. 2002; SUN et al. 2002; REN et al. 2010; SUN et al. 2002). The diverse insect fauna collected from all regional localities of the Yixian Formation consists of 16 orders, 149 families, and ca. 440 species (LIU et al. 2009; REN et al. 2012). The abundant plant groups include Equisetales, Filicales, Coniferales, Cycadales, Bennettitales, Czekanowskiales, Corystospermales, Caytoniales, a broad diversity of Ginkgoales and other ginkgophytes, Gnetales and a few species of angiosperms (DING et al. 2001; SUN et al. 2001; ZHENG et al. 2003). Of the 995 plant specimens collected and identified at Dawangzhangzi, *L. boii* consists of 343 specimens and was the dominant species (34.5%). A species of *Czekanowskia* was the subdominant taxon. Paleobotanical data from fossil palynomorphs and plants indicate a warm, moist climate (DING et al. 2001, 2003a,b; ZHENG et al. 2003; DING & ZHANG 2004).

Although numerous plants and insects have been described from the Yixian Formation, there are few plant-insect associational studies from China (POTT et al. 2012;

DING et al. 2013; NA et al. 2014). This study represents one of several current examinations of plant-insect interactions in the mid Mesozoic fossil record of northeastern China. However, more adequate, comparative databases are needed to achieve a broader, ecologic synthesis of plant-insect associations and their plant hosts within a paleocommunity context (LABANDEIRA & CURRANO 2013).

3. Materials and methods

Specimens from the bulk floral collections at Capital Normal University from Dawangzhangzi and other localities were evaluated for all plant taxa and all insect-mediated damage during 2010–2011, using the damage-type system for assessing the qualitative and quantitative extent of herbivory (WILF et al. 2001; LABANDEIRA et al. 2007). From this first, comprehensive dataset that listed insect damage types (DTs) on all plant-host specimens, the *Liaoningocladus boii* specimens from Dawangzhangzi and nearby Yixian localities were pooled into a second, more targeted dataset for investigating plant-insect interactions from specimens of *L. boii*, *Lindleycladus lanceolatus* (Lindley & Hutton) Harris, 1979 and *Podozamites lanceolatus* Braun 1843 (Q. Ding et al. unpubl. data). This second dataset of the three, mid-Mesozoic, broadleaved conifer taxa included material from two localities of the 40 million-year-old, latest Middle Jurassic Jiulongshan Formation of northeastern China. A subset of this second dataset, consisting only of *L. boii* specimens from Yixian Formation localities, formed a third, more narrowly focused dataset used for evaluations of all insect damage, including the leaf mine type and associated DTs only on the 343 specimens of *Liaoningocladus boii*, overwhelmingly from the Dawangzhangzi locality. It is this third dataset that provided source data for the current study. From the third dataset we identified all DTs on *L. boii*, but our focus for this report is on the single leaf-mine DT and two associated DTs.

Since gut contents and coprolites of herbivorous insects were largely unavailable as evidence for herbivory on Yixian plants, examination of various features of plant damage was instrumental to determine the presence of herbivorous insects (LABANDEIRA 2002). Within this broad category, we used several determinative criteria, including: (1) reaction rims such as callus on excised foliage; (2) micromorphological features, including necrotic flaps of tissue and extension of resistant vascular tissue (veinal stringers) into presumptively consumed areas; (3) highly stereotyped damage patterns inconsistent with detritivory; (4) secondary fungal infection of the leaf lamina adjacent to a leaf excision, a sign that live plant tissue was consumed; and (5) antiherbivore plant-host structures, such as thick cuticles. Any one of these types of evidence can be confirmatory in establishing

the presence of herbivory (the consumption of live plant tissues), such as leaf mining, as opposed to detritivory (consumption of dead plant and other tissues) (WILF et al. 2001; LABANDEIRA & CURRANO 2013).

We included oviposition as an informal type of “herbivory,” as this interaction represents the use of live plant tissues as a resource by an insect. In the case of oviposition, it is the ovipositor rather than the mouthparts that is the point of contact with the utilized plant. Notably, oviposition has a significantly documented fossil record similar to that of piercing and sucking, which is its counterpart in the mouthpart damage record (LABANDEIRA 2006a).

All plant specimens, with and without damage, were observed using a Leica M165C stereomicroscope. Plant specimens determined to have insect-mediated damage were photographed by a Nikon D100 camera for macro-photography and a Leica MZ12.5 stereomicroscope connected to a Nikon DXM1200C camera for microphotography. Images subsequently were processed with Adobe Photoshop CS2 and Corel-DRAW-12 software. Recorded data of fossil locality, specimen number, morphotype, damage type and comments were stored on Microsoft Office Excel spreadsheets for analyses. All specimens are housed as vouchers at the Key Laboratory of Insect Evolution & Environmental Changes at the College of Life Science, Capital Normal University (C.N.U.), in Beijing, China.

4. Results

Fourteen of the 343 total specimens of *Liaoningocladus boii* overwhelmingly from the Dawangzhangzi locality bore a distinctive leaf-mine damage type, or DT, representing an incidence of occurrence of 4%. (Some occurrences represent multiple leaves that are organically connected and are considered a single specimen.) This DT is defined and established as new DT280. DT280 is the most abundant single damage type for *L. boii* and corresponds to a morphologically unique leaf-mine feeding mode on *L. boii* within the regional Yixian Biota. A new ichnotaxon name is proposed for this distinctive leaf-

mining type. In a related issue, a context is established for recognizing the damage-type suite concept for linking DT280 to other DTs presumably caused by the same leaf-mining species.

4.1. Systematics

4.1.1. *Fossafolia* ichnogen. nov. Figs. 2, 3

Etymology. From the Latin: *fossa*, which signifies “mine,” “tunnel” or “channel”; and *folium*, the Latin word for “leaf.” The gender is feminine.

Type ichnospecies. *Fossafolia offae* ichnosp. nov.

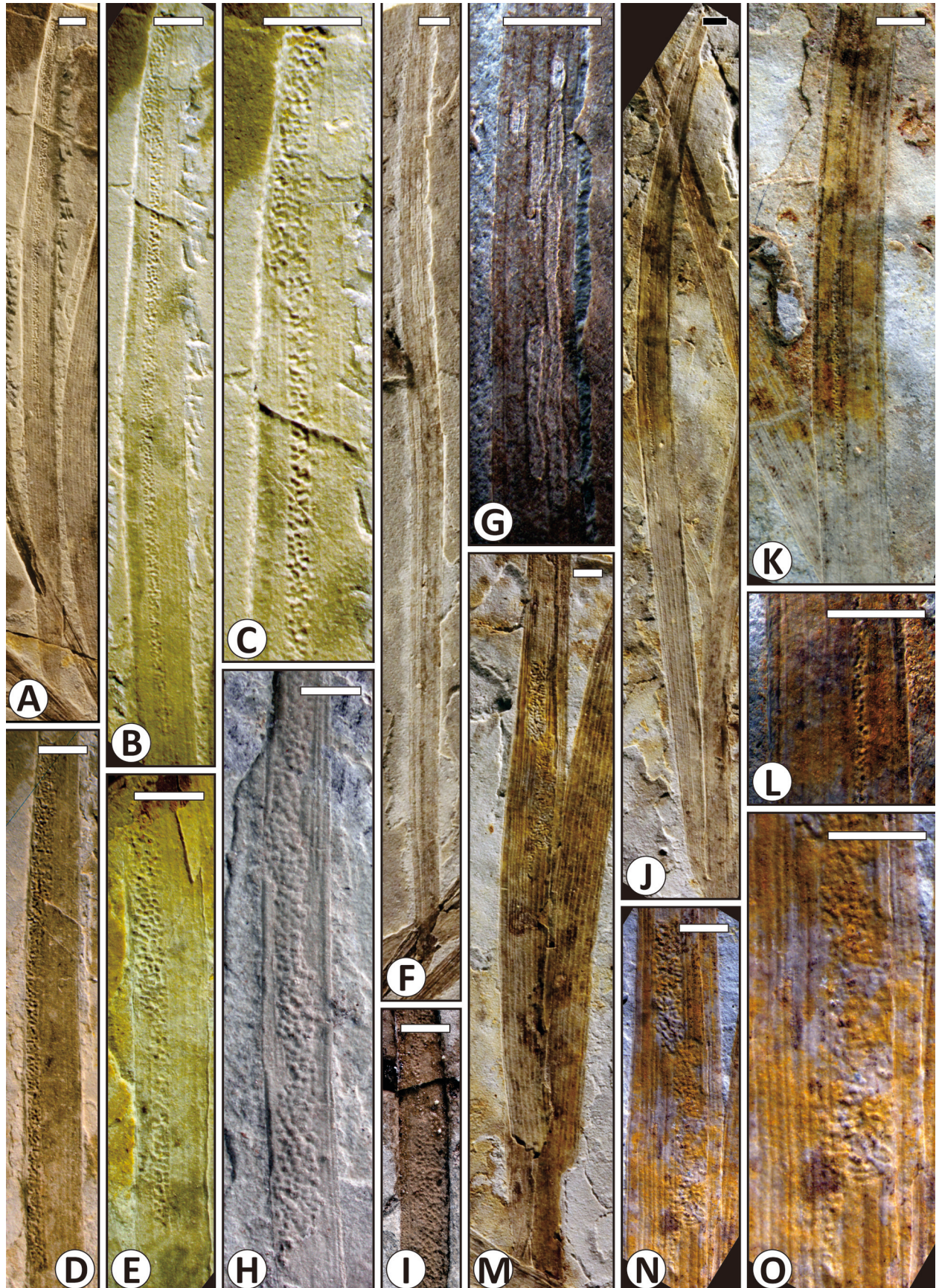
Description. Distinctive, full-depth, medium-length leaf mines with a tightly looped, intestiniform frass trail occurring on broad, multiple- and parallel-veined, entire-margined conifer leaves. One unbranched mine originates from an oviposition site of one or multiple eggs; later consisting of 3–5 mine width increments between the initial hatched egg and possible pupal chamber at mine terminus (Fig. 3C). Mine consists of earlier, linear, narrow mine phase constrained by primary venation that represent first and second width expansions by the larval instar (Fig. 2F,G,J–L); later, a wider, blotch-like mine phase delimits major increases in mine width in the third and fourth instar that often cross-cut primary venation during major mine expansion (Fig. 2A–E,H,I,M–O). Frass is characterized by occasional spheroidal pellets in early instars, but become more dense in the latter mine trail; similarly, the frass is characterized by a loosely (early phase) to tightly (late phase), sinusoidal, looping trajectory with each loop abutting onto preceding and succeeding loops during the late phase (Fig. 2C,H,I,L,O). The late phase becomes a tightly looping, intestiniform frass trail; a pockmarked appearance occurs particularly in later mine-width increments.

Diagnosis. Early-phase mines (first two mine-width expansions) occurring on *Liaoningocladus boii* resemble in overall form and contents DT71 mines present on *Heidiphyllum elongatum* from the Late Triassic (Carnian

→ **Fig. 2.** Digital photographic images of *Fossafolia offae* ichnosp. nov., a beetle leaf mine (DT280) on leaves of the conifer *Liaoningocladus boii* Sun, Zheng & Mei, 2000 (SUN et al. 2000), from the mid Early Cretaceous Yixian Formation in northeastern China. Late-phase (mature) mines are indicated in A–E, H, I and M–O; early-phase (immature) mines are at F, G and J–L. **A, B, C:** A late-phase mine under different magnifications; holotype CNU-PLA-LL-2010-062P-1-1. An overlay drawing of this mine showing details is provided in Fig. 3C. **D:** A late-phase mine; CNU-PLA-LL-2010-062P-1-2. An overlay drawing of this mine showing details is provided in Fig. 3D. **E:** A late-phase mine; CNU-PLA-LL-2010-062P-1-3. An overlay drawing of this mine showing details is provided in Fig. 3E. **F, G:** An early-phase mine; CNU-PLA-LL-2010-031-1-1. **H:** A late-phase mine; CNU-PLA-LL-2010-100-1-1. **I:** A late-phase mine; CNU-PLA-LL-2010-067C-3-1. **J, K, L:** An early-phase mine; CNU-PLA-LL-2010-116C-1-1. An overlay drawing of this mine (L) showing details is provided in Fig. 3A. **M–O:** A late-phase mine; CNU-PLA-LL-2010-116C-1-2. An overlay drawing of this mine (O) showing details is provided in Fig. 3B. (Scale bars: 2 mm throughout)

of the Karoo Basin in South Africa; SCOTT et al. 2004; LABANDEIRA 2006a). By contrast, early-phase mines generally are confined between two, adjacent, major veins

on *L. boii*, while the leaf mines on *H. elongatum* exhibited greater crossing over of major veins (ANDERSON & ANDERSON 1989; LABANDEIRA 2006a, 2012). In addition,



the late-phase mine (last two mine-width expansions) in this study consisted of a blotch-like condition that occasionally was preceded by a mine trajectory forming a 180° turn (Figs. 2A–E, 3C). However, *Triassohyponomus dinmorensis* mines – also on *H. elongatum* but from the Middle Triassic of Australia (ROZEFELDS & SOBBE 1987) – together with DT71 mines, are mostly longer and rectilinear in trajectory, not blotch-like, and have barely detectable mine width expansions compared to *F. offae* (ROZEFELDS & SOBBE 1987; LABANDEIRA 2012). *Triassohyponomus* and DT71 mine types mostly show a relatively constant mine width, whereas *L. boii* mines increase demonstrably in width (ROZEFELDS & SOBBE 1987; LABANDEIRA 2012).

The frass trail of DT71 is loosely (early mine phase) to tightly (later mine phase) sinusoidal (LABANDEIRA 2012). Although the *L. boii* mine, *Triassohyponomus* and DT71 have an intestinform frass trail, the thickness and tight sinuosity of looping are different (ROZEFELDS & SOBBE 1987; LABANDEIRA 2006a). The *L. boii* mine has a thicker and tighter frass trail than *Triassohyponomus*, and no coprolites or other material is evident in the frass trail of *Triassohyponomus* mines (ROZEFELDS & SOBBE 1987). SCOTT et al. (2004) figured a similar leaf mine on a Late Triassic seed fern, *Dejerseya lunensis*, also a linear mine from the Molteno formation, but no detailed descriptions were given. Several other, undescribed leaf mines are known from the Molteno Formation (LABANDEIRA et al. 2013) The *L. boii* mine is distinguished from other similar, mid-Mesozoic fossil leaf mines particularly in its distinctive frass-trail morphology, buttressing its status as a new ichnogenus.

Remarks. Similar leaf mines have been reported from the Blackstone Formation in southeastern Queensland (ROZEFELDS & SOBBE 1987) and the Molteno Formation in South Africa (SCOTT et al. 2004; LABANDEIRA 2006a, 2012; LABANDEIRA et al. 2007), Gondwanan deposits of Late Triassic age. *Fossafolia offae* superficially resembles leaf mines from these localities, particularly those on *Heidiphyllum elongatum*, a broad-leaved voltzialean

conifer (ANDERSON & ANDERSON 1989) that has no close phylogenetic relationship with *L. boii*. The earlier, Late Triassic leaf mines were named *Triassohyponomus dinmorensis* (ROZEFELDS & SOBBE 1987) and may be the same as DT71 of LABANDEIRA (2006a). Similar, undesignated and unnamed leaf mines occur in Kyrgyzstan during the slightly earlier Middle Triassic (ZHERIKHIN 2002), and are thought to be the earliest credible leaf mines (LABANDEIRA 2006a). It is notable that *H. elongatum* and *L. boii* are conifer leaf isomorphs that are broad, entire-margined, lanceolate leaves, with parallel major and minor veins widely attached to a stem. *Heidiphyllum* is a medium-sized, pole-like shrub with simple side branches bearing leaves on short shoots, whereas *Liaoningocladus* resembles a more typical, larger sized woody conifer with complexly bifurcating side branches that lack short shoots (ANDERSON et al. 2007; SUN et al. 2000). It appears that these leaf mines were made by similar leaf miners, most likely beetles that attacked similarly constructed leaves, but on the physiognomically different plants of *H. elongatus* and *L. boii*. Nevertheless, the Late Triassic leaf miner of the Molteno Formation also mined a wide variety of other penecontemporaneous seed-plant hosts, including Cycadales, Crystospermales and Ginkgoales (LABANDEIRA et al. 2013), unlike the miner of the single plant host of Early Cretaceous *L. boii*.

4.1.2. *Fossafolia offae* ichnosp. nov.

Figs. 2, 3

Etymology. From the Latin, *offa*, which means “pellet.”

Holotype. CNU-CON-LL-2010-062P/C-1-1 (Fig. 2A–C).

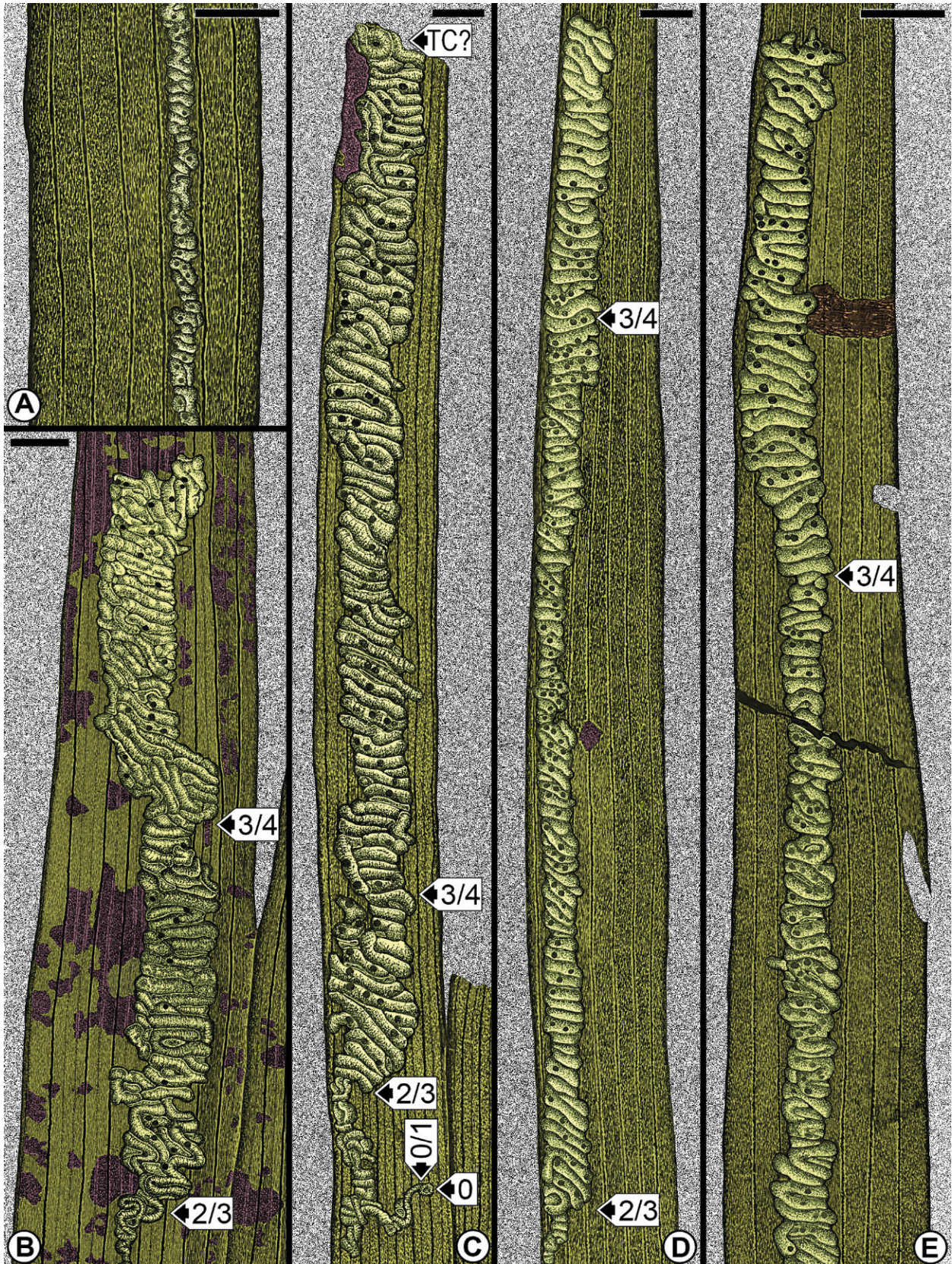
Plant host. *Liaoningocladus boii* (Coniferales incertae sedis) (Fig. 4A).

Description. Complete mine occupying 1/2 to 2/3 of leaf length. Mine consisting of four ca. unequal-width segments separated by three, significant mine-width increas-

→ **Fig. 3.** Enlarged overlay drawings of *Fossafolia offae* ichnosp. nov., a new beetle leaf mine (DT280) on the conifer *Liaoningocladus boii* Sun, Zheng & Mei, 2000, as they may have appeared during life. All mines are from the Dawangzhangzi locality in Liaoning Province, in northeastern China and originate from the Yixian Formation of latest Barremian age. Colors: olive green indicates unaltered leaf tissue; light green, mined tissue; purple, probable fungal damage; brown, extraneous woody plant material; stippled gray, surrounding matrix. Inferred instar stages and shifts: O, oviposition site; O/1, eclosion of the first instar larva from the egg; 1/2, shift from the first to the second larval instars; 2/3, shift from the second to the third larval instar; 3/4, shift from the third to fourth larval instars; and TC? displaying the mine terminus that houses possibly the discoid pupal chamber. Dark, circular, randomly occurring structures within the frass are coprolites. **A:** Probable second instar mine. Note mine confinement between two, adjacent, major primary veins. See Fig. 2L, CNU-PLA-LL-2010-116C-1-1. **B:** Leaf mine consisting of larval instars 2–4, with shifts between instars 2/3 and 3/4 indicated. Note the major offset of mine to the left, caused by larval breaching of two major veins, and spotty fungal colonization of the leaf’s surface. See Fig. 2O; CNU-PLA-LL-2010-116C-1-2. **C:** The most complete mine of *L. boii*, displaying an oviposition site (O), four mine width increases and associated structural changes (O/1, 1/2, 2/3, 3/4) by larval instars 1–4, and a possible pupal case at the mine terminus, where it is bordered by a linear fungal blotch at upper-left. Note the expansion of the third instar mine into three, additional, major interveinal areas at bottom. See Fig. 2B, CNU-PLA-LL-2010-062P-1-1. **D:** Leaf mine consisting of larval instars 2–4, with instar shifts 2/3 and 3/4 indicated. See Fig. 2D, holotype CNU-PLA-LL-2010-062P-1-2 (part) on a different leaf than (E). **E:** Linear leaf mine consisting of larval instars 2 and 3, with instar shift 2/3 indicated. See Fig. 2C, holotype CNU-PLA-LL-2010-062P-1-2 (part) on a different leaflet than (D). (Scale bars: 1 mm)

es, divided into an early phase (mine width increments 1 and 2) and a late phase (width increments 3 and 4) that occur singly (Fig. 2J–L) or multiply (Fig. 2F–G) on same leaf, typically confined between two adjacent major parallel veins that are separated by ca. 0.3 mm. Early

phase of mine immediately after eclosion (first width increment) threadlike, linear, barely displaying frass trail and generally lacking detectible coprolites; later mine (second width increment) more robust, linear in overall trajectory, with minor, irregular frass-trail erratically



looping but no or few observable coprolites. Late-phase mines occur singly on leaves; mostly with an irregular margin and blotch-like form; occasionally reversing direction 180° and crossing major veins (Figs. 2A–E, 3C); mine width 0.5–1.2 mm or broader, occupied entirely by tightly looping, intestiniform frass trail; encompassing all of mine width (Fig. 2H–I, M–O). Spheroidal fecal pellets (coprolites) often preserved, embedded in frass trail; individual pellets (coprolites) ca. 0.08 mm in diameter for early-phase mines; ca. 0.13 mm diameter for late-phase mines (Fig. 2C, E, H, L, O). Frass trail consisting of pellets encompassed by fluidized excreta, and likely unconsumed tissue fragments (Fig. 3B–D). No apparent reaction rim present at contact between later phase mine and adjacent leaf tissue. Oviposition site obscure to evident, represented by DT101 damage. Circular pupal chamber possibly present.

Holotype CNU-CON-LL-2010-062P/C-1-1 (Fig. 2A–C): Nearly complete, linear mine, 28.5 mm in length, originating 20 mm from leaf base, coursing to leaf tip; inferred mine origin 0.5 mm wide, extending to a length of 23.5 mm toward leaf center; at least one major vein crossed; mine terminus width 1.0 mm, occurring for 5 mm along margin at leaf tip; mine crosses several major veins; intestiniform frass trail preserved, pellets ca. 0.13 mm diameter.

Paratype CNU-CON-LL-2010-062P/C-1-2 (Fig. 2D): A single, overall, linear, late-phase mine, 13.3 mm by 17.9 mm from the leaf base, extending to leaf tip; inferred origin 0.5 mm wide, coursing 5.6 mm to leaf center, cross-over of at least one major vein; last mine instar 1.0 mm wide, length 7.7 mm, occupying leaf margin near leaf tip, with several major veins crossed over; frass preserved, pellets 0.13 mm diameter.

Paratype CNU-CON-LL-2010-062P/C-1-3 (Fig. 2E): Single, overall linear, early- and late phase mine, 21.6 mm long, originating 20.5 mm from the leaf base, extending to leaf tip, occupying leaf margin throughout; inferred origin 0.5 mm wide, length 14.9 mm long, crossing over at least one major vein; last instar 1.0 mm wide, length 6.7 mm, crossing over several major veins; frass preserved, pellets 0.13 mm diameter.

Paratype CNU-CON-LL2010031-1-1 (Fig. 2F–G): Multiple early-phase mines positioned in parallel fashion to each other; each mine linear and narrow, strictly confined between two major veins towards leaf center; 0.3 mm in width, lengths 1.6–32.3 mm; frass poorly preserved; probable oviposition site preserved adjacent one mine.

Paratype CNU-CON-LL2010100-1-1 (Fig. 2H): Single, late-phase, blotch-like mine, originating 10 mm from leaf base, and running partly along leaf margin; ca. 1.5 mm wide, 20 mm long; crossing over several major veins; frass preserved, pellets 0.1 mm diameter.

Paratype CNU-CON-LL2010067P/C-3-1 (Fig. 2I): Single, late phase, blotch-like mine on a leaf fragment of *L. boii*; 1.5 mm wide, 27.3 mm long; positioned entirely along leaf margin; frass preserved, pellets 0.13 mm diameter.

Paratype CNU-CON-LL2010116P/C-1-1 (Fig. 2J–L): Single, overall linear, early-phase mine; originating 29.3 mm from the leaf base; strictly confined to two major veins toward leaf center; 0.3 mm wide and 25 mm long; frass preserved, pellets 0.08 mm diameter.

Paratype CNU-CON-LL2010116P/C-1-2 (Fig. 2M–O): Single, overall linear to blotch-like mine; originating 26.5 mm from leaf base, trajectory partly along leaf margin; 14.9 mm long, consisting of three obvious width expansions: first linear, 0.3 mm wide, strictly confined to two major veins, 1.7 mm long toward center of leaf; second portion blotch-like, about 1.4 mm wide, along leaf edge, crossing over several major veins, extending to 7.7 mm long; third mine segment blotch-like, ca. 1.4 mm wide, coursing to leaf center and again crossing over several major veins and 9.8 mm long; frass preserved, pellets 0.13 mm diameter.

Remarks. Several aspects of the mine morphology allow interpretation of some basic larval habits. Four percent of the *Liaoningocladus boii* leaves were leaf mined. Ten of the 23 leaves constitute early-phase only mines, interpreted as created by larval instars 1 and 2; five leaves had multiple mines (Fig. 2F, G). All late-phase mines, interpreted as formed by larval instars 3 and 4, occurred singly on a leaf. Whether the mines were single or multiple on a leaf, early-phase mines occurred at some distance from the leaf margin (Fig. 2F, G, J–L). By contrast, late-phase mines were deployed partly or entirely along the leaf margin (Fig. 2A–E, H, I, M–O). Among early-phase mines, only two single mines contained barely recognizable, smaller-sized, spheroidal pellets which were tightly embedded within a fluidized frass trail (Fig. 2J–L), a type of feeding typical of sap-consuming larvae. One of the leaves bore multiple mines that appeared to house an adjacent oviposition site or entrance site (Fig. 2G).

4.2. Affiliated damage types: The DT280–DT101–DT103 damage-type suite

Dawangzhangzi *Liaoningocladus boii* specimen CNU-CON-LL-2010-149P-1 displays the distinctive oviposition of DT101. This oviposition mark (Fig. 4D) is similar in shape, size, location and arrangement to a probable oviposition mark preserved on *F. offae* specimen CNU-CON-LL-2010-031-1-1 (Fig. 2F, G). Twelve other occurrences of DT101 are known from the 343 specimens of *L. boii*. These oviposition marks were inserted endophytically (within plant tissue), placed singly between two adjacent main veins, and are elongate-lenticular to ellipsoidal in shape (Fig. 4B–D). A typical size for an oviposition mark is, 1.43 mm long x 0.25 mm wide (Fig. 4B); other DT101 oviposition marks exhibit very little variation in these dimensions. Ovipositional reaction tissue was distinct for several of the oviposition marks (Fig. 4D, arrow).

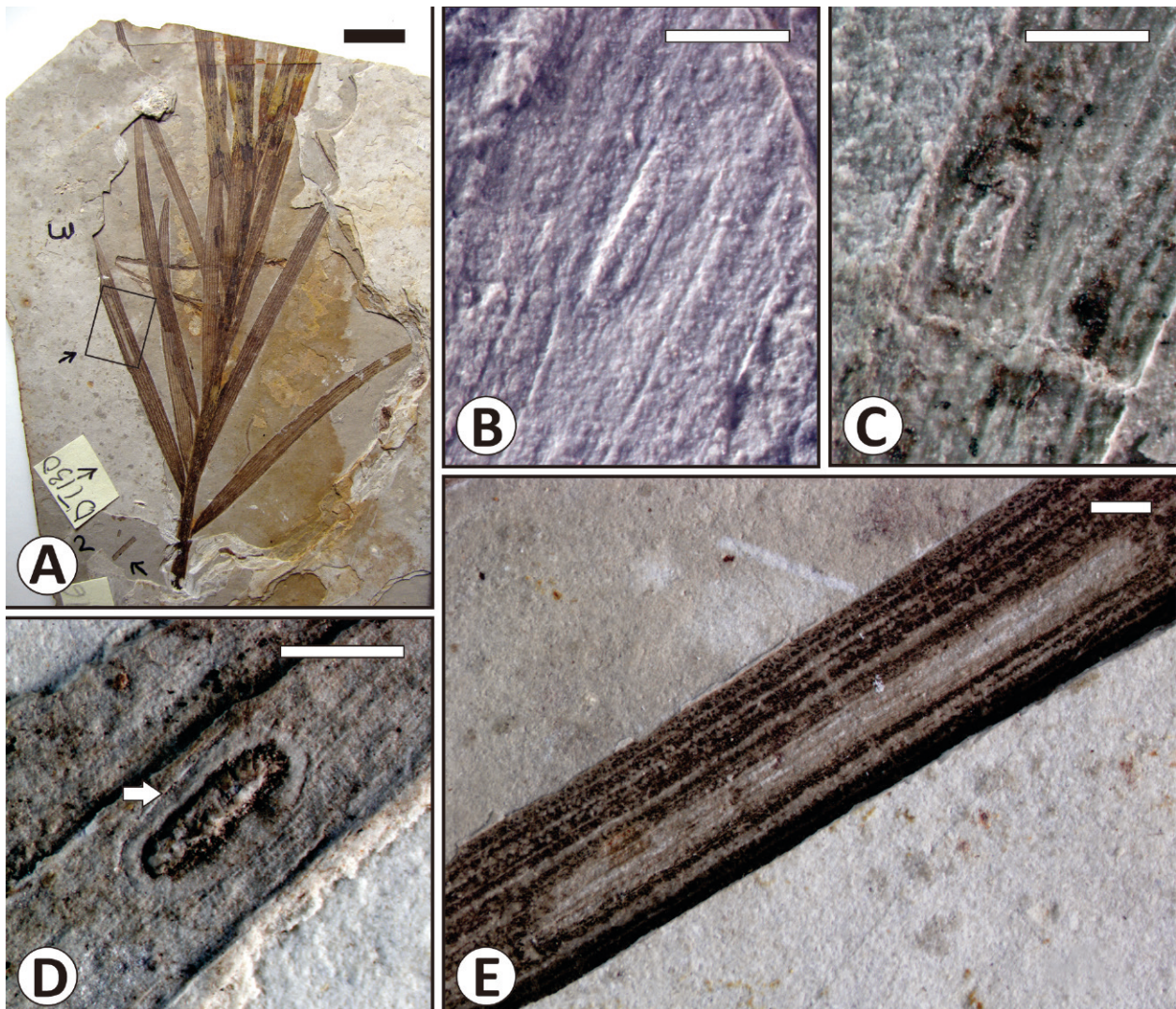


Fig. 4. The affiliated multidamage type assemblage of DT280-DT103-DT101 on *Liaoningocladus boii* Sun, Zheng & Mei, 2000, from the Yixian Formation of northeastern China. **A:** *Liaoningocladus boii* CNU-PLA-LL-2010-230-1, the plant host of the multidamager suite of DT280 leaf mining (Figs. 2 and 3), DT101 oviposition (B–D) at right and lower-left, and DT103 surface feeding (E) at lower-right, all presumably caused by the same insect herbivore. An enlargement of surface feeding (DT103) in the rectangular box at center-left is enlarged in (E). **B:** An oviposition mark of DT101 on *L. boii*, CNU-PLA-LL-2010-282P-1. **C:** A second oviposition mark of DT101 on *L. boii*, CNU-PLA-LL-2010-388-1. **D:** A third oviposition mark (DT101) on *L. boii*, CNU-PLA-LL-2010-149P-1. Arrow points to reaction rim. **E:** Window feeding and surface abrasion (DT103) on *L. boii*, enlarged from (A) at upper-left, CNU-PLA-LL-2010-230-1. (Scale bars: (A) 2 cm, (B)–(E) 2 mm).

Distinctive surface-feeding damage of DT103, consistent with that of an adult beetle, has been observed on *L. boii* (Fig. 4A,E). Because of the association between DT103 and DT280 on *L. boii*, also occurring elsewhere on different leaves, there is a strong suspicion that the adult of the leaf-mining species also is the culprit for DT103 feeding damage. The association of the DT101, DT103 and DT280 is considered a linked damage-type series, or a *damage type suite*, and constitutes a hypothesis for further examination if corroboration of these three damage types is sustained on the same host plant across sites of the Yixian Formation. If corroborated, this damage-type suite would constitute evidence by a culprit for a multiuse strategy that accessed *L. boii* foliar resources for oviposition, leaf mining and external feeding.

5. The likely leaf miner: morphologic, phylogenetic and fossil evidence

Three broad categories of evidence are relevant for taxonomic identification of the insect leaf miner on *Liaoningocladus boii* that created *Fossafolia offae*, synonymous with DT280 damage.

(1) The leaf mine features of *L. boii* was compared to various leaf mines made by particular, modern leaf-mining lineages based on a detailed description of the fossil mine structures. The extensive primary literature of

modern leaf mining was consulted to establish the likely identity of *F. offae*. Journal-based sources with detailed accounts of leaf mines, accompanied by photographic documentation, were sought. The 21 volume set of *Minen-Herbarium* (HERING 1929) also was consulted, which contains pressed foliage of modern European leaf mines with identifications of plant hosts and insect leaf miners.

(2) Phylogenetic data were used to constrain the time of origin of a suspect leaf-mining lineage, such that its presence could reasonably have produced the leaf-mine of interest during the mid Early Cretaceous. Evidence from phylogenetic relationships of the clades and subclades in question has the potential to limit culprit presence or absence to a specified time interval. Such an approach can exclude particular clades if they are shown from phylogenetic analyses to have originated (significantly) after the 125-million-year-old deposit was laid down.

(3) The occurrence of the suspected fossil lineage in the same deposit, or in a spatiotemporally close context, provided additional support for a likely match. The presence or absence of candidate fossils in the relevant fossil deposit was the most direct way to ascertain whether a particular culprit group was present at a specified time and region of concern. Fortunately, the Yixian Formation has a rich record of potential fossil insect lineages, including a broad array of beetle species (TAN et al. 2010).

Potential leaf-mining lineages are confined to the four, major, holometabolous clades of Diptera, Lepidoptera, Hymenoptera and Coleoptera (CONNOR & TAVERNER 1997; SINCLAIR & HUGHES 2010), all of which could provide potential candidates for attributing *Fossafolia offae* to a particular, lower-ranked leaf-mining clade. Therefore, each of the three types of evidence above, (1)–(3), is presented under each of these four suspect taxa, with discussions of particular leaf-mining lineages that may have been responsible for creation of *F. offae*.

5.1. Diptera, Lepidoptera and Hymenoptera

5.1.1. Evidence from modern leaf-mining lineages

Since dipteran leaf miners tunnel through plant tissue on their left and right sides, dipteran mines have trails of frass adpressed to one side that alternates with frass confined to the opposite side. Dipteran leaf mines often have several such left or right transitions with the same mine (WINKLER et al. 2010). In addition to (1) right–left segmented frass trails, dipteran mines typically are (2) not full-depth in terms of tissue consumption, preferring a single layer of foliar tissue, and (3) have oviposition sites that are accompanied by nearby small, ovipositional pricks noticeable on the plant host's epidermis (WINKLER et al. 2010). These distinctive features (HERING 1951;

SPENCER 1990) are absent from moth (Lepidoptera), sawfly (Hymenoptera) and beetle (Coleoptera) mines. Dipteran leaf miners have a more recent fossil record; their earliest occurrence in the fossil record is during the mid-Paleocene (WINKLER et al. 2010).

Lepidopteran leaf mines exhibit significantly different life-history patterns than that of *Fossafolia offae*. Major differences that set lepidopteran mines apart from *F. offae* include: (1) gracile mines frequently confined to the epidermis; (2) a loosely organized, mostly fluidized frass trail that lacks solid fecal pellets; (3) mines typically producing 3–13 instars particularly in early-appearing lepidopteran leaf-mining lineages; (4) evidence for use of silk in construction of the mine from the earliest to latest instars; (5) mostly circular, epidermal openings of exit holes of less than 5 mm at the mine terminus; and (6) late instar, blotch-like phases that typically contain frass as long, thread-like strings (DYAR 1890; NEEDHAM et al. 1928; HERING 1951; KUMATA 1978; PUPLESIS 1994; ESPERK et al. 2007).

It is difficult to attribute *F. offae* to a hymenopteran leaf-mining clade of the “Symphyta” (sawflies). Many mines of sawflies and beetles appear similar. However, leaf-mining larvae of the “Symphyta”: (1) overwhelmingly have five or six instars (SMITH 1993; ESPERK et al. 2007); (2) produce large, conspicuous blotch mines that traverse most of the leaf-tissue on a leaf, and often occupy the foliar area between the midrib and leaf margin; and (3) contain scattered, clustered or otherwise disorganized agglomerations of fecal pellets (NEEDHAM et al. 1928; HERING 1951; CSÓKA 2003).

By contrast, coleopteran leaf-mining taxa typically consist of 3–5 larval instars. *F. offae* has several additional features consistent with beetle and not sawfly leaf mining. These coleopteran features include: (1) the absence of silk in construction of the feeding phase of the mine; (2) a full-depth leaf mine; (3) a very tortuous frass trail with densely packed frass; and (4) a linear mine present to the second or possibly third instar stages, followed by a considerable mine width expansion resembling an unconstrained, blotch-like formation (HERING 1951). Collectively, these data would be most consistent with assignment of *F. offae* to a coleopteran fabricator.

5.1.2. Phylogenetic evidence

For varied reasons, the Diptera, Lepidoptera and Hymenoptera can be ruled out, on phylogenetic grounds, as culprits for *Fossafolia offae* damage on *Liaoningocladus boii*. For the Diptera, leaf-mining lineages are associated with the origin and diversification of the Cyclorhapha during the latest Late Cretaceous, including the earlier appearance of the subclade Phoroidea in the mid Late Cretaceous (LABANDEIRA 2005). The Cyclorhapha retains the overwhelming bulk of leaf-mining lineages within the Diptera, consisting of nine separate, leaf-mining lineages, of which the Agromyzidae (leafmining flies) currently are prominent worldwide (SPENCER 1990;

WINKLER et al. 2010). Although the Agromyzidae is the lineage to which all fossil dipteran leaf mines have been attributed, it has a spotty fossil record (CRANE & JARZEMBOWSKI 1980; GIVULESCU 1984; WINKLER et al. 2010), having a well-established earliest occurrence in the middle Paleocene of Montana, U.S.A. (WINKLER et al. 2010). Consequently, the clade encompassing the Agromyzidae, the Schizophora, likely originated during the latest Cretaceous (WINKLER et al. 2010), far postdating the *F. offae* occurrence in the mid Early Cretaceous. The middle Paleocene mine, *Phytomyzites biliapchaensis*, is very distinctive, as are other cyclorrhaphan mines fabricated by mouthhook-bearing larvae, and cannot be confused with the mines of other leaf-mining insects (WINKLER et al. 2010). Parenthetically, there are four clades of nematocerous Diptera that have rare, leaf-mining species (LABANDEIRA 2005), but these lineages are relatively derived and occur in geochronologically ephemeral contexts such as small, mid-oceanic islands (SWEZEY 1915), indicating geologically recent derivations.

By contrast, leaf-mining clades of Lepidoptera undoubtedly were present during the Late Cretaceous (KOZLOV 1988; LABANDEIRA et al. 1994; SOHN et al. 2012), and were represented by the clade Glossata (WHALLEY 1978; WAHLBERG et al. 2013; ZHANG et al. 2013). To date, two body-fossil occurrences of potentially glossate Lepidoptera are known from the mid Mesozoic. The first is a presumptive member of Incurvariidae (fairy moths) that constructed distinctive circular-case-forming mines (DAVIS 1999) that appear very different from the mine *F. offae*. A second lineage is represented by *Protolepis cuprealata* Kozlov, 1989 that may extend the presence of the leaf-mining Glossata 25-million-years earlier, into the Late Jurassic (KOZLOV 1989; SOHN et al. 2012; ZHANG et al. 2013). It is highly likely that a few lineages of Glossata were present during the Early Cretaceous, and could have been responsible for *F. offae*. However, none of these Early to Late Cretaceous lepidopteran lineages, including the somewhat more recent Nepticulidae and Gracillariidae produce shallow, single-tissue mines (LABANDEIRA et al. 1994; DAVIS 1999) that could have produced a full-depth mine resembling *F. offae*.

Several lineages of the early-appearing group of Hymenoptera, the paraphyletic “Symphyta” (SHARKEY 2007; RONQUIST et al. 2012), were present during the Early Cretaceous (GAO et al. 2010). Many lineages of this assemblage extend to the Middle Jurassic (RASNITSYN 1975; RASNITSYN & ZHANG 2004), and the conifer-pollen-feeding Xyelidae (xyelid sawflies), the most plesiotypic extant clade (RONQUIST et al. 2012), was present during the Middle Triassic (RASNITSYN 1964). Existence of the “symphytan” clade Siricidae (horntails) in Middle Jurassic strata of northeastern China (RASNITSYN & ZHANG 2004) indicates, by phylogenetic inference, that the Tenthredinoidea (common sawflies and relatives) (HEITLAND & PSCHORN-WALCHER 1993) were present for tens of millions of years before deposition of the Yixian beds. Consequently, “symphytan” leaf-mining lineages, many of which are suspected to have participated in a variety of

associations with ferns and gymnosperms (HEITLAND & PSCHORN-WALCHER 1993), are candidates for the producer of the *F. offae* leaf mine during the mid Early Cretaceous.

5.1.3. Fossil evidence

Fossils of the Diptera and Hymenoptera are well represented during the Mesozoic of northeastern China (ZHANG et al. 2010; GAO et al. 2010), whereas fossils of the Lepidoptera are much less abundant (ZHANG et al. 2013).

For the Diptera, the fossil record of the Yixian Formation and other mid-Mesozoic localities of eastern Eurasia lack members of the Cyclorrhapha. These deposits contain only nematocerous and brachycerous lineages that lack significant leaf-mining taxa either as fossils or in the modern record (HERING 1951, 1957; WINKLER et al. 2010; but see LABANDEIRA 2005).

Likewise, the Yixian Formation lacks lepidopterans, and thus do not contribute to leaf-mining candidates. However, the older Jiulongshan Formation does contain several lepidopteran species attributable to the lineages Eolepidoptergidae, Mesokristenseniidae and Ascidolediptergidae (HUANG et al. 2010; ZHANG et al. 2013), but they probably lacked leaf-mining habits. The broader region of eastern Eurasia contains fossil specimens of the Micropterigidae and Eolepidopterigidae (COCKERELL 1919; RASNITSYN 1983; SKALSKI 1979, 1984; KOZLOV 1988, 1989), bearing pollen crushing, mandible-bearing clades which are closely related to the early-appearing, leaf-mining lineage of the Glossata. Additionally, fossil evidence exists for the Glossata during the mid Early Cretaceous (WAHLBERG et al. 2013), a clade which, with the exception of nonglossate, mandibulate Heterobathmiidae (KRISTENSEN & NIELSEN 1979), consists of many leaf-mining taxa. The Glossata currently are absent from the Jiulongshan or Yixian Formations, or elsewhere in mid-Mesozoic eastern Eurasia (ZHANG et al. 2013, but see KOZLOV 1989). The absence of lepidopteran leaf-mining lineages during the mid Mesozoic of Eastern Eurasia may signify the absence of this group until the mid Cretaceous, about 35 million years later (KOZLOV 1988), after the Yixian Formation was deposited.

The mid Mesozoic, eastern Eurasian fossil record of the Hymenoptera is robust, and the Yixian Formation is no exception (GAO et al. 2010). The record consists almost entirely of “symphytan” and parasitoid groups (GAO et al. 2010), but it is the “Symphyta” (sawflies, a paraphyletic group) (M. WANG et al. 2013; GAO et al. 2013), such as Tenthredinidae (common sawflies) (ZHANG 1985), that would provide a role as leaf miner of *Liaoningocladus boii*. Given the habits of modern sawflies (SMITH 1993), it is not likely that any Yixian fossil “symphytan”, typically with stereotypical wood-boring larvae such as Xyelidae, Sinosiricidae, Xyelotomidae, Praesiricidae and Cephidae, would have been capable of producing *Fossafolia offae* leaf mines. Based on fossil evidence from the Yixian Formation, the most likely leaf miner was the tenthredinid *Palaeathalia laiyangensis* (ZHANG 1985), given

what is known of the biology of modern Tenthredinidae (ALTENHOFER & PSCHORN-WALCHER 2006).

5.2. Coleoptera

5.2.1. Evidence from modern leaf-mining lineages

Modern leaf-mining Coleoptera are affiliated principally with the four major lineages of Buprestidae, Mordellidae, Chrysomelidae and Curculionoidea. The less common superfamilies of Bostrichoidea and Cucujoidea, as well as clades typically not associated with leaf mining in the Chrysomeloidea and Curculionoidea (NEEDHAM et al. 1928; HERING 1951; CONNOR & TAVERNER 1997; SANTIAGO-BLAY 2004), have recently documented leaf mining species for which little is known of their mine morphologies. These leaf-mining taxa come from lineages typically not associated with leaf mining, such as the Ptiniidae, Nitidulidae, Cerambycidae, Scolytinae and Platipodinae (PHILIPS et al. 1998; KATO 1998, 2001; MARTIN 2000; SANTIAGO-BLAY 2004; CLINE et al. 2014). These leaf mines almost always occur in late-appearing taxa that very likely evolved considerably more recently than the age of the Yixian Formation.

5.2.1.1. Buprestidae is a globally distributed, diverse family of 14,800 species that occur in virtually all terrestrial habitats (NELSON et al. 2008). Adults predominantly feed on pollen, flowers, nectar, foliage and bark of angiosperms, but occasionally consume fungal spores (CHAPMAN 1923; LAWRENCE & ŚLIPIŃSKI 2013); larvae are dominantly wood borers that feed on cambial tissues of angiosperms and gymnosperms and subordinately are gallers, cone feeders and leaf miners (LAWRENCE 1991). Leaf miners of Buprestidae are univoltine or multivolt-

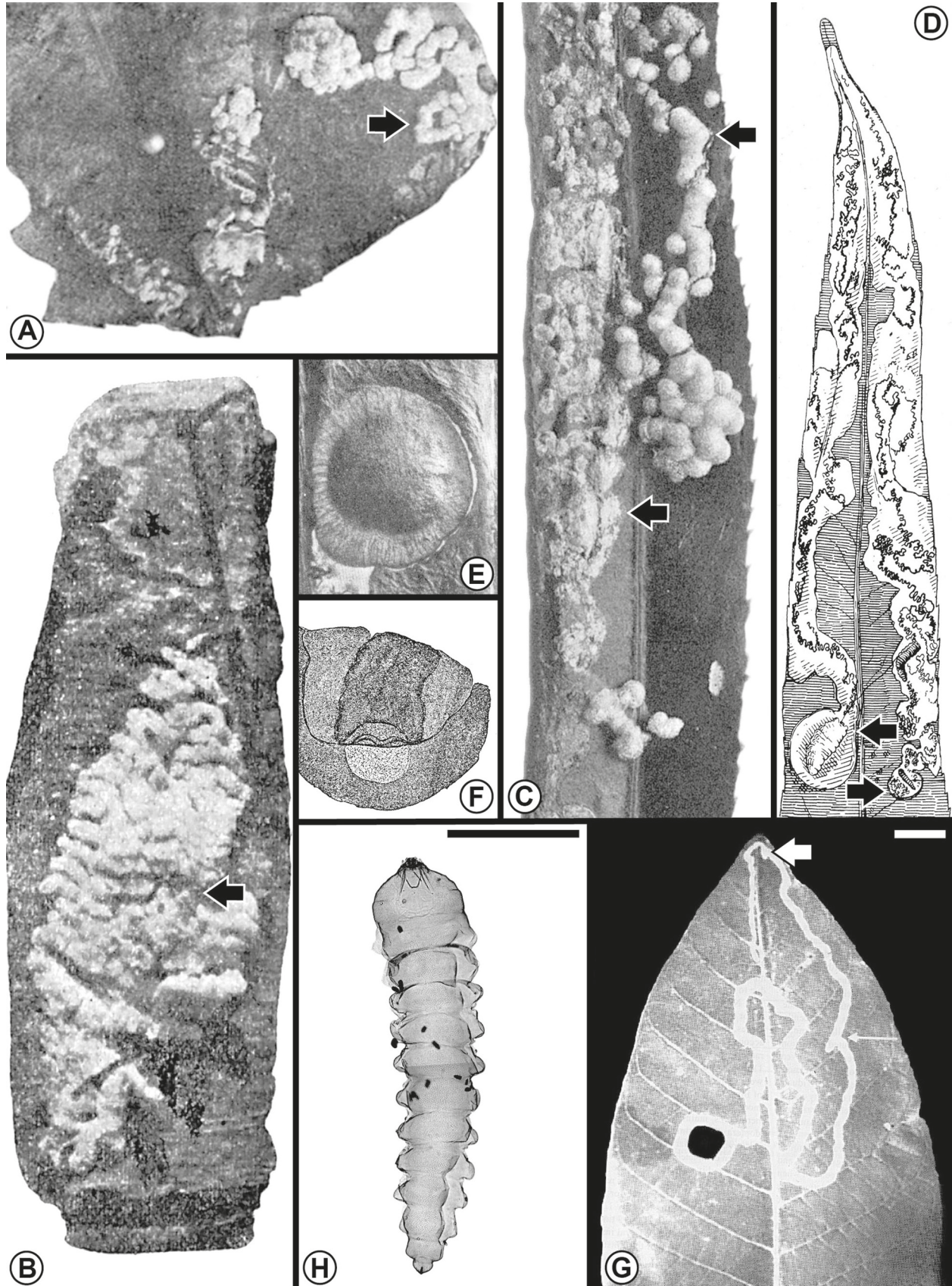
ine. Buprestid leaf-mining larvae are endophytic, mostly as wood borers, and have a legless, highly flattened body form with a retractile, prognathous head possessing reduced appendages. The head region bears robust, symmetrical bi- or tridentate mandibles equipped with massive mandible adductor and abductor muscles that occupy the expanded genal region of the head capsule (BENOIT 1964). Larvae range in length from 2 to 100 mm and undergo 3–5 larval instars. For example, three larval instars occur in *Pachyschelus psychotriae* (HESPENHEIDE & KIM 1993), *P. coeruleipennis* (QUEIROZ 2002), *Taphrocerus gracilis* (CHAPMAN 1923), *T. schaefferi* (STORY et al. 1979) and some species of *Trachys* (BÍLÝ 1993). Four instars are found in *Brachys ovatus* (CONNOR 1988), whereas congeneric *B. tessellatus* exhibits five instars (TURNBOW & FRANKLIN 1981; WADDELL & MOSSEAU 1996). In some species, such as *Pachyschelus psychotriae* (HESPENHEIDE & KIM 1992), the last larval instar is morphologically distinct from the preceding instars (GREBENNIKOV 2013), and consumes most of the leaf tissue. In one study of the three larval instars of *P. psychotriae*, HESPENHEIDE & KIM (1992) measured leaf-mine area consumed, and determined that the first to third larval instars proportionately consumed 9, 32, and 59%, of plant-host tissues.

Buprestid leaf-mine morphology is broadly similar across all mining taxa, although there are differences in the size, shape and tortuosity of mine as well as the deployment of frass within the mine. Although the leaf mines typically are linear, they can be wide and appear blotch-like (Fig. 5D), particularly during the last larval instar (FIEBRIG 1908; WEISS & NICOLAY 1919; KOGAN 1964b; HESPENHEIDE & KIM 1992; BÍLÝ 1993), and usually are full-depth tissue feeders (Fig. 5A–C), avoiding only epidermal and sometimes vascular tissues (CHAPMAN 1923; STORY et al. 1979; WADDELL & MOSSEAU 1996). However, in buprestid mining of thick leaves such as *Conarus panamensis* (Connaraceae), only certain tissue layers are mined (HESPENHEIDE & KIM 1992). Based on instar mine width, data measurements for nine spe-

→ **Fig. 5.** Leaf-mine features produced by modern *Pachyschelus* (Buprestidae) larvae on hosts *Sapium* and *Croton* (Euphorbiaceae) (A–G), and an example of a modern *Pachyschelus* larva (H). **A:** An opened leaf mine showing the frass structure produced by an undetermined species of *Pachyschelus* on host *Sapium glandulosum*, the gum tree. Black arrow points to probable second instar damage. From FIEBRIG (1908: p. 336, fig. 4). **B:** Another opened leaf mine as in (A), but showing a tightly sinusoidal, looping frass trail typical of the fourth larval instar. Black arrow points to one of several successive rows of sinusoidal fecal boluses perpendicular to slightly inclined to mine medial axis trajectory. From FIEBRIG (1908: p. 360, fig. 12). **C:** An opened mine of *P. undularius* on host *S. glandulosum*, as in figures (A) and (B), showing the earlier stages of mine development, including probable first instar, fecal frass trail at upper right (black arrow) and probable beginning of the third instar at lower left (black arrow). From BRUCH (1917: plate 1, fig. 2). **D:** A drawing of the same host and miner as in (C), displaying two complete mines, one on each side of the dividing leaf midrib. At bottom, the left-directed arrow points to a larva within its discoid pupal chamber in the process of pupation; the right-directed arrow points to a mining larva at some time prior to pupation. From BRUCH (1917: plate 2, fig. 2). **E:** Pupal disc made by the same miner and in the same host as (C), enclosing a fourth-instar larva undergoing pupation, showing the same structure as in the lower left of (D) and in (F). From FIEBRIG (1908: p. 338, fig. 6). **F:** A mine terminus with circular pupal disc as in (D) and (E), representing the same miner and host as (A). From FIEBRIG (1908: p. 338, fig. 6). **G:** A leaf from crushfoil, *Croton floribundus*, showing the course of a complete mine, including the 180° turn at leaf apex (white arrow) and discoid pupal chamber at lower left of the leaf miner *P. coeruleipennis*. (Scale bar: 10 mm) From QUEIROZ (2002: p. 71, fig. 1), reprinted, with permission from a creative commons agreement from the Instituto Internacional de Ecología. **H:** Shed cuticle of a fourth-instar larva of *P. laevigatus* from a leaf of tick trefoil, *Desmodium glutinosum* (Fabaceae). (Scale bar: 1 mm) From GREBENNIKOV (2013: p. 167, fig. 1L), reprinted with permission from the Institute of Entomology, Academy of Sciences, Czech Republic.

cies representing the tribes Brachyini and Pachyschelini, mine widths develop in distinct width increments. Mine widths for the first instar are a threadlike 0.5–1.0 mm; the second or third instars in those species with a fourth instar larva are 1.0–4.0 mm; and the final instar mine

width is highly variable, often blotch-like, with 4.0–14.0 mm (Fig. 5D,G) (WEISS & NICOLAY 1919; KOGAN 1963, 1964b; STORY et al. 1979; HESPENHEIDE & KIM 1992; QUEIROZ 2002). In *Pachyschelus psychotriae* and *P. coeruleipennis*, the mine typically courses along the midvein



of its host *Connarus panamensis*, turns 180° near the leaflet tip, and then proceeds to the leaf base (HESPENHEIDE & KIM 1992), a feature found in several buprestid leaf-mining species (Fig. 5G).

Wood-boring Buprestidae have an ovipositor specialized for considerable extension and insertion of eggs into deep crevices and bark fissures (BEER 1949). By contrast, leaf-mining buprestids have three, quite different oviposition strategies. The most common and widely mentioned method is simple placement of an egg or cluster of eggs on a leaf, usually at the upper surface and often along a major vein or leaf margin, after which the eggs are covered by a waxy or tar-like substance (WEISS 1954; TURNBOW & FRANKLIN 1981; CONNOR 1988; WADDELL & MOSSEAU 1996; FOX et al. 1997; MACRAE 2004). This condition is found in *Taphrocerus* and most species of *Trachys* and *Brachys*. A second mode of oviposition involves modification of the host-plant epidermis prior to oviposition through scraping by the mouthparts or by the edge of the fifth abdominal sternite, resulting in a shallow pit, followed by oviposition of an egg or egg cluster into the newly-formed depression and sealing by a layer of whitish excrement (SUBRAMANIAM 1920; TURNBOW & FRANKLIN 1981; ZAKA-UR-RAB 1991). This pattern of oviposition occurs in some species of *Trachys* and *Brachys*. The third mode, found in *Pachyschelus*, involves insertion of the ovipositor into an incision that penetrates the epidermis and underlying parenchyma. This incision leaves a noticeable ellipsoidal, lenticular or circular lesion, into which the eggs are deposited (FIEBRIG 1908; BRUCH 1917; WEISS & WEST 1922; KOGAN 1963, 1964a). This is consistent with the DT101 structure on *Liaonin-goeladus boii*.

Buprestid leaf-mining frass trails are distinctive. The mine frass is produced in a tightly compressed, sinusoidal fashion as broad, transverse loops, where the orientation of each frass stream within the mine is perpendicular to slightly inclined to the mine medial axis (Fig. 5B; FIEBRIG 1908; BRUCH 1917; HERING 1942; KOGAN 1963). Individual bolus streams of fecal material tend to have a bulbous appearance, with denser fecal pellets embedded within the fecal stream (Fig. 5A–C) (FIEBRIG 1908; BRUCH 1917). Towards the end of the mine, particularly the phase produced by the fourth instar larva, each frass loop cuts into the preceding loop (Fig. 5B), resulting in occupation of the full width and depth of the mine (FIEBRIG 1908; BRUCH 1917). The frass contains fecal pellets that are irregularly positioned in a curvilinear fashion or occasionally are more clustered (Fig. 5C). Individual fecal pellets are spheroidal to ellipsoidal, but infrequently may have a stringy appearance. The mine terminus is not enlarged, and its width is a continuation of the last larval instar; however, in some taxa, such as *Pachyschelus*, a flattened, near perfectly circular, discoid pupal chamber is present that houses the last-instar larva as it transitions to a pupa (Fig. 5E,F) (BRUCH 1917; HESPENHEIDE & KIM 1992). In some instances the last-instar larva exits the mine from a pupal case attached by silken threads to the leaf surface (HESPENHEIDE & KIM 1992); in other taxa,

pupation occurs in or barely within the soil (WEISS & NICOLAY 1919; NICOLAY & WEISS 1923). For some groups pupation can occur without an enclosure and the imago emerges from the mine by cutting a hole in the upper epidermis (SUBRAMANIAM 1920) or by a slit at the bottom of the mine (WEISS & NICOLAY 1919; STORY et al. 1979).

The Buprestidae are classified into the subfamilies Polycestinae, Buprestinae and Agrilinae, the first two of these almost exclusively consist of species with wood-boring larvae on conifers and angiosperms. Within the Agrilinae, larvae of the tribes Coraebini and Agrilini are exclusively wood boring, whereas the tribes Aphanisticini (*Aphanisticus*) and Trachini (*Trachys*, *Neotrachys*, *Brachys*, *Taphrocerus*, *Leiopleura*, *Pachyschelus*) are exclusively leaf mining species (NELSON et al. 2008). A common understanding is that the leaf-mining habit appeared after the wood-boring habit was established (FROST 1924; WEIDLICH 1986; BERNARD et al. 2005), although it is more likely that leaf mining is as old as wood boring based on sister-group relationships of the major wood-boring and leaf-mining clades.

Aphanisticus, a major genus of Aphanisticini, typically consists of poorly known species that mine monocot hosts. For example, *A. cochinchinae* occurs on various Poaceae (gamagrass, sugarcane) and Cyperaceae (sedges) (SUBRAMANIAM 1920; CHANG & OTO 1984; WELLSO & JACKMAN 1995; MACRAE & NELSON 2003). Within Trachyini, the subtribe Trachyina contains the taxa *Trachys* and *Neotrachys* (NELSON et al. 2008), the former of which have colonized a variety of mostly woody dicotyledonous hosts, particularly the Malvaceae (mallows), Rosaceae (roses spiraeas and stone fruits) and Salicaceae (willows and cottonwoods) (SUBRAMANIAM 1920; HERING 1929, 1957; WEISS 1954; ZAKA-UR-RAB 1991). By contrast, species of *Neotrachys* exclusively leaf mine ferns, particularly the Gleicheniaceae and Cyatheaceae, often *Cnemidaria* tree ferns (HESPENHEIDE 1980, 1982, 2006).

The Trachyini subtribe Brachyina consists of *Brachys* and *Taphrocerus* (NELSON et al. 2008). *Brachys* species occur on a broad spectrum of plants, including dicots and monocots, but mostly mine woody hosts. *Brachys* has formed leaf-mine interactions with the Fagaceae, especially *Quercus* and *Fagus* (NICOLAY & WEISS 1923; TURNBOW & FRANKLIN 1981; WADDELL & MOSSEAU 1996; FOX et al. 1997; WADDELL et al. 2001), other hardwoods, such as *Inga*, *Acer*, *Carya*, *Populus*, and *Ulmus* (NEEDHAM et al. 1928; HERING 1942; KOGAN 1964a), and less woody taxa that includes various bamboos and *Calea* (HERING 1942; KOGAN 1964b). *Taphrocerus* is less well known, and like *Aphanisticus*, occurs on monocot hosts. Known leaf-miners target a wide variety of sedges (CHAPMAN 1923; STORY et al. 1979; MACRAE 2004). The Trachyini subtribe Leiopleurina consists of the sole leaf-mining genus *Leiophlura*, whose plant host remains unknown (COBOS 1978; NELSON et al. 1981).

Perhaps the most studied leaf-mining buprestid is *Pachyschelus* from the Trachyini subtribe Pachyscheliina. It mines a variety of woody dicot trees, especially the Euphorbiaceae, such as *Croton* and *Sapium* (FIEBRIG

1908; BRUCH 1917; VOGT 1949; HERING 1960; OBENBERGER 1960; KOGAN 1963; QUEIROZ 2002), but also the hardwoods *Serjania*, *Luehea* and *Connarus* (FISHER 1929; HERING 1942, KOGAN 1963; HESPENHEIDE & KIM 1992), and occasionally herbaceous Fabaceae, including *Lespedeza* and *Desmodium* (FIEBRIG 1908; KNULL 1920; WEISS & WEST 1922).

5.2.1.2. Mordellidae consists of ca. 1500 species worldwide whose adults feed on flowers, accessing particularly pollen and nectar (LAWRENCE & ŚLIPÍŃSKI 2013). Larvae are endophytic but overwhelmingly are pith borers and to much less extent leaf miners; a single case of gall inquilinism also is known (PING 1915; LENGKEREN 1922; FORD & JACKMAN 1996). The larvae are largely host specific and target softer tissues, such as pith parenchyma in composites (Asteraceae), but also bore into the more hardened tissues of arborescent, woody hosts of Fagaceae, Sapindaceae, Juglandaceae and Tiliaceae (FORD & JACKMAN 1996). The biogeographically extensive *Mordellistena* is probably the dominant stem- or twig borer lineage within the family, and its pith borings have been documented on the composites *Helianthus* and *Artemisia*, the grasses *Spartina* and *Uniola*, and the dogbane *Apocynum* (SCHWARZ 1887; KLAUSNITZER 1967; FRANCISCOLO 1974; STILING & STRONG 1983; VOICU & IVANCIA 1996). Apparently, it is also the only lineage containing leaf-mining larvae, the distinctive mine of *M. epidendrana* on the orchid *Cattleya labiata* being the best-documented example (LENGKEREN 1920, 1922; RAY 1937). The thick, parallel-veined leaves of *C. labiata* house asteronome mines (HERING 1951), characterized by a narrow, central “feeder” mine from which originate, often in a radiating pattern, similarly narrow, lateral branch mines that end in cul-de-sacs (LENGKEREN 1922: figs. C, G). Clearly, the leaf mines of the Mordellidae are quite different from *Fossafolia offae*.

5.2.1.3. Chrysomelidae is a very diverse clade of 32,500 species (LAWRENCE & ŚLIPÍŃSKI 2013) that have eclectic feeding habits, including external foliage feeding, pith boring, galling, seed predation, pollen feeding and leaf mining (SANTIAGO-BLAY 2004). Unlike other major beetle leaf-mining clades such as the Buprestidae, Mordellidae and Curculionoidea, where the mining habit originated several times via concealed feeding under bark or as pith borings in stems, it appears that leaf-mining Chrysomelidae arose via leaf feeding, undoubtedly several times (SANTIAGO-BLAY 2004). The leaf-mining habit is more abundant than in any other beetle lineage (CONNOR & TAVERNER 1997; SINCLAIR & HUGHES 2000). Consequently, the leaf-mining habit in sublineages of Chrysomelidae apparently is not a plesiomorphic trait, but rather is an apomorphic condition (SANTIAGO-BLAY 2004; also see CONNOR & TAVERNER 1997). There are relatively few leaf-mining species across the more early-appearing and later-appearing clades; the greatest speciosity occurs in subclades of the more derived Cassidinae (tortoise beetles) including the paraphyletic “Hispiniae” (leafmining

beetles) (HESPENHEIDE 1991; CONNOR & TAVERNER 1997).

Concentration of leaf mining taxa in the Cassidinae occurs in both the Old World and New World as separate, tribal-level lineages, where it apparently originated separately in these disparate biogeographic areas (SANTIAGO-BLAY 2004). Leafmining Cassidinae, the “Hispiniae,” mine (near-exclusively) monocots, particularly palms, screw-pines, grasses, sedges, ginger, bananas and heliconias (UHMANN 1934; GRESSITT 1957, 1960, 1963), many of which have architecturally stout, parallel veins. Other chrysomelid taxa, such as tortoise-beetles, mine dicots including Malpighiaceae (nances), Verbenaceae (vervains), Bignoniaceae (bignonias), Tiliaceae (lindens), Sterculiaceae (chocolates), Malvaceae and Sapindaceae (soapberries and maples) (UHMANN 1934; SANTIAGO-BLAY 2004), and occasionally ferns (KATO 1991). Leaf mining more rarely occurs in other chrysomelid subfamilies and targets basal angiosperm lineages appearing or thought to have originated during the Early Cretaceous, particularly Nymphaeales, Piperales, Ranunculales and Proteales, the latter included in core dicots (WILF et al. 2000). Evidently chrysomelid external feeding in general is associated with early angiosperm diversification, but the leaf-mining lineages appeared considerably later during the latest Cretaceous and Paleogene (but see GÓMEZ-ZURITA et al. 2007).

Chrysomelid leaf mines have a fairly uniform and broadly stereotyped set of defining features that occur in hosts as different as ferns and monocot and dicot angiosperms. They display feeble, early-mine serpentine phases followed by a massive, blotch phase that often is approximately equidimensional in length and width and frequently engulfs earlier, serpentine mine phases (NICOLAY & WEISS 1918; UHMANN 1934; HERING 1951, 1957; KATO 1991). The disposition of the particulate frass generally is loose, often clustered, but rarely undulatory to tightly sinusoidal in trajectory, likely a result of larvae consuming one tissue stratum rather than being a full-depth tissue consumer (HERING 1929, 1960). Chrysomelid mines in monocots, however, typically are more linear (GRESSITT 1960, 1963), and are associated with more prominent and hardened tissues of parallel-oriented veins, but also retain the blotch-like aspect of the last larval instar.

5.2.1.4. Curculionoidea. Adults of basally diverging Curculionoidea subgroups, in particular the Nemonychidae Belidae, Attelabidae and Caridae (MCKENNA et al. 2009), are dominantly consumers of pollen and other reproductive tissues of cycads, conifers, angiosperms and to a lesser extent, ferns (CROWSON 1981; ARNETT et al. 2002; LIU & REN 2007). (Another basally diverging clade, the Anthribidae, overwhelmingly feed on fungi and is not considered further.) A noteworthy pattern is that the primary host-plants of modern Nemonychidae are the Araucariaceae (KUSCHEL 1983, 1994; FARRELL 1998; LIU et al. 2006a), which could be related to extinct, later Mesozoic conifers such as *L. boii* (G. Sun, pers. comm.), considering their very similar leaf structure. The adults and larvae of the Belidae and Nemonychidae share

the same host-plant, typically a conifer or a cycad, and even occur in the same strobilar tissues as their conspecific adults (ARNETT et al. 2002). Although most modern larvae of Nemonychidae are pollen feeders, other feeding associations are known, such as the wood-boring habits of *Cimberis elongates* (THOMAS & HERDY 1961). These life habits suggest that other forms of endophytic feeding, including leaf mining, could have originated among larvae of Nemonychidae from borer or other inner-tissue feeding modes (FROST 1924; CONNOR & TAVERNER 1997).

The Belidae are a biogeographically disjunct lineage whose larvae and adults currently are associated with hosts as diverse as ferns, cycads, conifers and angiosperms (VANIN 1976; MARVALDI et al. 2006). The belid subfamily Belinae, of Gondwanan distribution, consists of external foliage feeders on ground- and tree ferns (Blechnaceae, Cyatheaceae, Dryopteridiaceae, Polypodiaceae), arborescent conifers (Cupressaceae, Podocarpaceae), and dicot angiosperms (Sapotaceae) (HUDSON 1934; BONDAR 1947; KUSCHEL 1959; ZIMMERMAN 1994). There is no evidence for leaf mining in Belinae; although some have true endophytic larvae, but only as wood borers (KUSCHEL 1959; BRITTON 1970) that occur in wood, soft trunk tissues and fern petioles of dead or dying plants.

The belid subfamily Oxycoryninae has, like the Belinae, larval and adult feeding relationships with a wide variety of ferns and seed plants, prominently including conifers, and includes, to our knowledge, the only leaf-mining larvae known within the early appearing Curculionoidea. Among the four major Oxycoryninae lineages, larvae of one lineage specializes on palms and those of a second target podocarpaceous and cupressaceous arborescent conifers. A third lineage consists of host-specific consumers of parenchyma on gymnospermous strobilar tissues, feeding on reproductive tissues of Araucariaceae, and more particularly, the sporophylls of cycads such as *Zamia* and *Dioon*, or bizarrely, the inflorescences of dicot root parasites such the Hydnoraceae and Balanophoraceae (ANDERSON 1941; KUSCHEL 2003; MARVALDI et al. 2003, 2006). A fourth lineage is a frequent generalist on a broad spectrum of monocot and especially dicot angiosperms, and includes one specialist leaf-mining taxon. In this lineage, two species of the genus *Proterhinus* – *P. abnormis* and *P. phyllobius* – are leaf miners on the host *Broussaisia arguta* (Hydrangeaceae, an angiosperm) in uppermost montane forest on the island of Oahu in Hawai'i (SWEZEY 1913a,b). This endophytic life-habit is exceptional for larvae of *Proterhinus*, whose other species typically are external feeders. *Proterhinus abnormis* and *P. phyllobius* larvae are robust, legless and slightly C-shaped in lateral profile (ANDERSON 1941), but their mines on *B. arguta* (SWEZEY 1921: fig. 1) lack evidence for a full-depth mine. Rather, the mines of *Proterhinus* resemble those in which the epidermis or an upper single-tissue stratum was consumed. *Proterhinus* mines are very different from *Fossafolia offae*.

In Attelabidae, with ca. 2000 species (HAMILTON 2002), the larvae of Attelabinae have evolved diverse,

leaf-modifying behaviors with plants (HALL & BUSS 2012; KOBAYASHI et al. 2012). These habits include petiolar leaf excision, leaf rolling, leaf tying, and leaf mining that probably evolved from pith borings of cut shoots or petioles (HERING 1957; KOBAYASHI 2012). Attelabines mine a variety of hardwoods that include dead leaves of sassafras and kamahi (HAMILTON 1980; MAY 1992); the live leaves of *Fagus grandiflora*, in which a trumpet-shaped mine with extensive blotches is formed (HERING 1957; NIELSEN 1968; SWEENEY et al. 2012); *Chrysolepis* and other hardwoods resulting in a broad blotch mine occupying an entire half leaf (HERING 1957; AOKI et al. 2010); and *Symplocos* consisting of a mine with an early, short serpentine phase, followed by an extensive blotch (SAWADA 1994). The three larval instars typical of the group produce mines that expand considerably to the terminus, characterized by a blotch containing curvilinear but not sinusoidal frass trails (HERING 1957).

Of the Curculionidae, with over 60,000 species (LAWRENCE & ŚLIPINSKI 2013), ca. 25 genera are leaf miners on angiosperms. Some leaf-mining species produce stem borings and often associated leaf mines, consuming the softer tissues of emergent aquatic hosts such as *Hydrilla* and *Nymphaea* (MCGAHA 1952; BENNETT & BUCKINGHAM 2000). Many curculionid leaf miners are consumers of herbaceous terrestrial angiosperms affecting hawkweed, hawksbeard, centaury, mustard and garlic (BUHR 1954, 1956; HERING 1957). Angiosperm shrubs and trees, for example *Betula*, *Fagus*, *Cytisus* and *Tchihatchewia* similarly are leaf mined by Curculionidae (HERING 1957; KOROTYAEV & GÜLTEKIN 2003). Curculionid mines are spatulate in overall aspect, and have an early serpentine phase that rapidly expands from a wide mine to a large, conspicuous blotch (NEEDHAM et al. 1928; BUHR 1954, 1956; HERING 1951, 1957). The last larval instar typically produces a notable, often elongate but otherwise circular, lobate to variously shaped blotch. Frequently placed to one side of the terminal blotch is a dark, thickened, well-defined circular area indicating the pupation site. The frass trail is situated as a recognizable, medial line during the first two or three larval instars, but becomes increasingly diffuse in later instars as fecal pellets are produced in clusters or dispersed singly in localized areas of the blotch. The frass trail assumes a loose, undulatory trajectory in later instars that is rarely tightly sinusoidal. In some instances the last instar that forms the blotch encompasses and obliterates previously made damage to the leaf.

5.2.2. Phylogenetic evidence

All four leaf-mining clades were likely present by the mid Late Cretaceous at 125 Ma, as supported by a fossil-calibrated, “all compatible” consensus tree (HUNT et al. 2007). The buprestid-containing clade (Buprestoidea) was established at 217.0 ± 10.92 Ma (mid Late Triassic), with 10 reconstructed lineages present during the mid Early Cretaceous. Similarly, but with fewer data, the Mordellidae was established during the Middle Jurassic

and only a few lineages, mostly stem groups, are present by mid Early Cretaceous time (HUNT et al. 2007). The common stem lineage to the Curculionoidea and Chrysomelidae originated at 171.5 ± 27.06 Ma by the early Middle Jurassic (HUNT et al. 2007), for which there is a fossil occurrence in the Jiulongshan Formation at 165 Ma (ZHANG 2005). By the mid Early Cretaceous, the encompassing Chrysomelidae + Curculionoidea clade was represented by eleven lineages (HUNT et al. 2007). Other, more finely-resolved, fossil-calibrated studies indicate that the Chrysomelidae was represented by eight reconstructed lineages (FARRELL 1998), and the Curculionoidea, including the occasionally leaf-mining Belidae, Attelabidae and Curculionidae, were represented by nine (FARRELL 1998) or twelve (MCKENNA et al. 2009) lineages. These analyses suggest that all four coleopteran lineages of Buprestidae, Mordellidae, Chrysomelidae and the relevant sublineages of the Curculionoidea were present by 125 Ma.

5.2.3. Fossil evidence

The Coleoptera of the Yixian Formation consist of 20 families and somewhat more than 80 species (REN et al. 2012). Yixian lineages present for placement of *F. offae* are (1) Buprestidae (Fig. 6), (2) Mordellidae (including Liaoximordellidae), (3) Chrysomelidae, and (4) Curculionoidea, the Belidae and Attelabidae (GROMOV et al. 1993; GRATSHEV & ZHERIKHIN 2000; LIU et al. 2007, 2008; KIREJTSHUK et al. 2010; TAN et al. 2010; REN et al. 2012; DAVIS et al. 2013). Evidently, there are no known Curculionidae from the Yixian Formation (LEGALOV 2012; DAVIS et al. 2013). These four major, family-ranked taxa contain sublineages which have descendants that currently are leaf-miners (CROWSON 1981; SANTIAGO-BLAY 2004). Notably, some of these taxa also are present in the 40-million-year-old, nearby Jiulongshan Formation, that include the Buprestidae (HONG & WANG 1990; KIREJTSHUK et al. 2010; PAN et al. 2011), Mordellidae (WANG 1993; WANG & ZHANG 2011; B. WANG et al. 2013) and Chrysomelidae (ZHANG 2005). The Belidae apparently were absent in the Jiulongshan Formation, although they are highly diverse in the intervening Late Jurassic deposits at Karatau, Kazakhstan (LEGALOV 2012; B. WANG et al. 2013). Fossils of the Attelabidae remain unknown.

Buprestidae have a fair fossil record throughout western Eurasia (Table S1 in Electronic Supplement). For Middle and Late Jurassic deposits, buprestid fossils occur in southern Kazakhstan, northeastern China and central-south Russia. For Early Cretaceous deposits, there are occurrences in northeastern China, throughout Mongolia and south-central Russia. For the earlier Late Cretaceous, fossils occur in southern Kazakhstan, eastern Russia and northern Burma. Buprestid fossils from these localities generally are not assigned to subfamilial groups, such as the Agrilinae, that strongly would indicate a leaf-mining life habit. Affiliations have been made, however, to the Buprestinae (PONOMARENKO 1971), whose modern lar-

vae are obligate wood borers (NELSON et al. 2008), and to the Parathyreinae (ALEXEEV 1993, 2000), with larvae of unknown feeding habits. *Trapezitergum grande*, from the Liutiaogou locality in Inner Mongolia of the Yixian Formation (Fig. 6A,B), is placed in Buprestinae (YU et al. 2013), and three other additional species from the older Jiulongshan Formation in Parathyreinae (PAN et al. 2011). These three latest Middle Jurassic species of Jiulongshan *Sinoparathyrea* (Fig. 6C–F) indicate a modest speciosity of Buprestidae from the immediate region ca. 40 million-years before the Yixian deposits were laid (PAN et al. 2011). In lieu of evidence to the contrary, it is possible that Parathyreinae larvae were leaf miners.

5.3. Evidence for the likely leaf miner of *Liaoningocladus boii*

Fossafolia offae is a leaf mine that is distinctive in overall shape and size, ovipositional site damage, confinement pattern by major veins, discrete mine-width increases (Fig. 3B–D), frass type, fecal coprolite size, and micromorphological mine features that display behavior. Based on these attributes, the most likely and available group of mid-Mesozoic, coleopteran leaf miners responsible for making *F. offae* was overwhelmingly the Buprestidae. The Mordellidae, Chrysomelidae and Curculionoidea-Belidae are highly unlikely to have made the mine. The three types of evidence presented above are based on: (1) structural features of modern leaf mines, (2) phylogenetic evidence for the presence of suspect culprit lineages, and (3) the presence of relevant fossil taxa considered to have made the mine within the same deposit or originating from a spatiotemporally nearby deposit. Based on these evaluative criteria, the most likely fabricator of the mine was a beetle of the Buprestidae, perhaps a taxon in Trachyini close to modern *Pachyschelus*. Currently, the best fossil candidate is the Yixian buprestid, *Trapezitergum grande* (YU et al. 2013), although its placement in the subfamily Buprestinae indicates that their larvae may have been a wood borer.

Some details are known of the larva that fed on *Liaoningocladus boii*. The larva consumed foliar tissue between the upper and lower epidermis and fabricated a distinctive, linear, largely vein-confined mine during an earlier instar phase which contrasted with a more blotch-like, vein-crosscutting, later-instar mine (Fig. 3). Adults of this beetle either fed on leaves of its larval plant host, *L. boii*, by producing linear patches of window feeding (DT103) (LOPEZ & HODDLE 2014), or alternatively but much less likely were pollinators that fed on gymnosperm reproductive structures. The adult female probably laid eggs singly into leaf tissues centered between adjacent major veins (DT101), from which emerged the leaf miner. These autecological observations provide additional evidence from which we conclude that the culprit species most likely was a buprestid beetle.

Other features also can be used to narrow the search for the culprit, such as larval size, behavioral characteristics of the leaf miner and the biology surrounding aborted mines. From the estimated size of the last instar larva based on the *F. offae* mine width, we infer that the adult leaf miner did not exceed 2 mm in body width, and was ca. 10 mm long. This relatively small size might be related to agility within the leaf mine, such as the 180° trajectory turn occurring in some *F. offae* mines (Figs. 2A–C, 3C). This behavior has a modern analog in *Pachyschelus coeruleipennis* (Buprestidae) (QUEIROZ 2002), a miner of the euphorb *Croton floribundus*, and *Cyperispa hypolytri* (Chrysomelidae), which mines leaves of comparable foliar architecture (GRESSITT 1957).

An additional behavioral feature found in *F. offae* was that earlier-instar and later-instar mines sometimes were not preserved on the same leaf, and thus represent an aborted mine or otherwise disruption of a leaf-mine developmental stage. In one instance, an early-phase mine was extremely abbreviated, about 2 mm in length (Fig. 2Q). Possible causes of leaf-mine abortion are that the mining larva was killed by a parasitoid, the leaf was shed by the plant, or the leaf miner experienced some external disturbance. In the two latter cases, cessation of mining may have been followed by a brief period of exposure, and subsequent resumption of leaf mining in another leaf (HERING 1951). Many larvae of leaf-mining Chrysomelidae are attacked by parasitoids, such as *Pharangispa purpureipennis* on *Costus* leaves and *Promecotheca papuana* on palm leaves (SANTIAGO-BLAY 2004; MARIAU 1975). Leaf-mining larvae frequently are immobilized by small, hymenopteran parasitoids, including a variety of larval endo- and ectoparasitoids and egg-parasitoids (GRESSITT 1957). Another instance was the beginning of a mid-phase mine, suggesting that a larva created a second, new mine. This habit exists in several species of extant Chrysomelidae, such as hispine Cassidinae, notably *Hispa testacea* on *Cistus salviaefolius* and *Chalepus dorsalis* on *Robinia pseudoacacia* (NEEDHAM et al. 1928). It also occurs in some Galerucinae that formerly were considered alceines (flea beetles) (CROWSON 1981).

The Buprestidae have been reported from the Yixian Formation (YU et al. 2013, 2014), but also from the forty-million-year older Jiulongshan Biota (PAN et al. 2011). It is thought that the Buprestidae originated during the Late Triassic (HUNT et al. 2007) and their larvae initially were

probably associated with gymnosperms as wood borers (WEIDLICH 1986). Leaf-mining within the Buprestidae may be a secondary life habit (WEIDLICH 1986; HESPENHEIDE 1991; CONNOR & TAVERNER 1997), and occurs to our knowledge only in the subfamily Argilinae (NELSON et al. 2008). The origin of leaf mining in the Buprestidae may represent a cladogenetic event that occurred by the mid Early Cretaceous. This novel feeding mode also incurred high host specificity and a proneness to extinction that was linked to the demise of its sole host, *Liaoningocladus boii*.

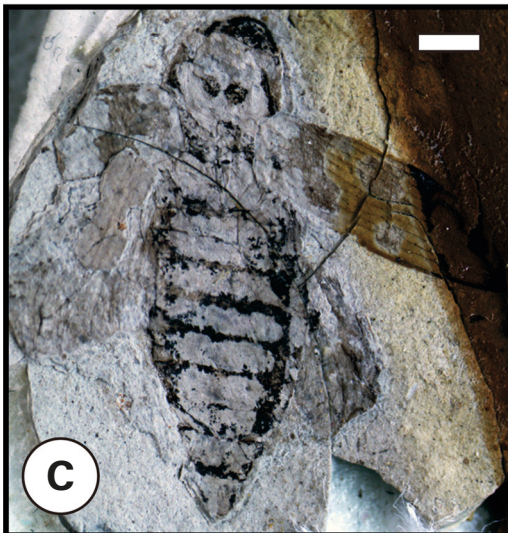
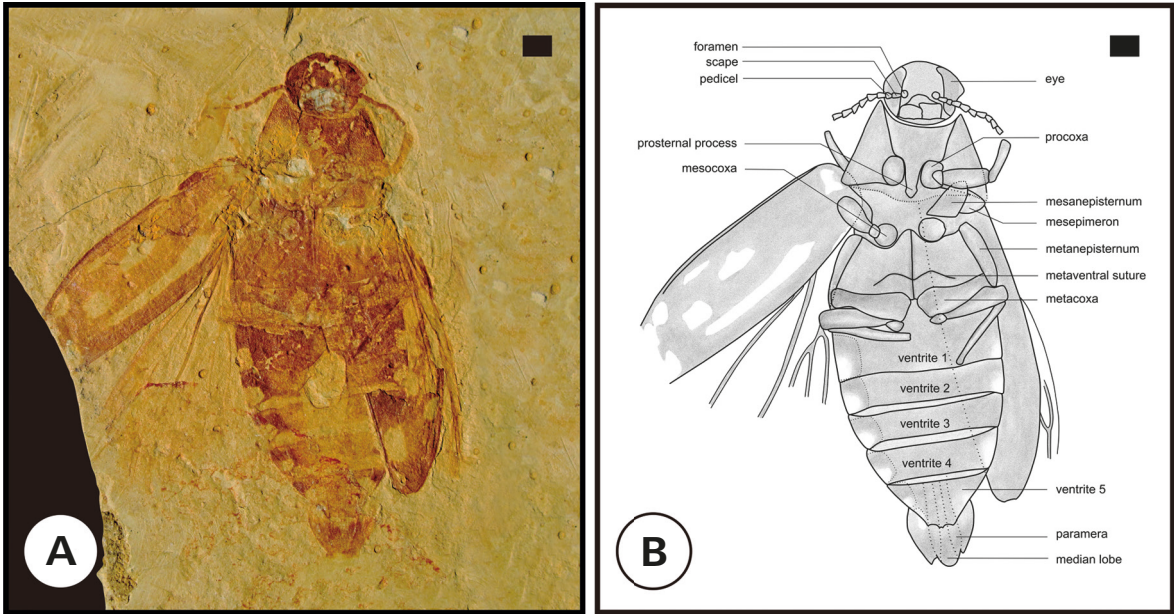
6. Discussion

In addition to establishment of explicit, objective criteria to better circumscribe the taxonomic affiliation of fossil insect leaf mines (mentioned immediately above), there are two, additional, derivative issues that flow from the discovery of a probable buprestid leaf miner in the mid Early Cretaceous Yixian Formation of northeastern China: (1) introduction of the concept of the damage-type suite into the vocabulary of plant-insect interaction studies, and (2) recognition of the increasing separateness of the preangiospermous and angiospermous plant-insect interaction records. This latter issue is an increasingly important issue that involves interpretation of fossils in amber and compression-impression deposits ranging from ca. 125 to 90 Ma as gymnosperm-hosted insect lineages were being replaced by newly originating insect lineages that developed associations with angiosperms (FARRELL 1998; LABANDEIRA 2006b, 2014a,b; WANG et al. 2013).

6.1. The Damage-Type Suite

The associated leaf-mining (DT280), oviposition (DT101) and surface feeding (DT103) damage on *L. boii* comprise a damage-type suite that circumscribes a single maker

→ **Fig. 6.** A buprestid species (A, B) of the mid Early Cretaceous Yixian Formation at the Dawangzhangzi Locality, near Lingyuan, Liaoning Province, China (YU et al. 2013, 2014), co-occurring in the same deposit as the leaf mines in Figs. 2 and 3. This or a related species may have been the likely culprit of the *Fossafolia offae* ichnosp. nov. (DT280) leaf mines on *Liaoningocladus boii*. **A:** *Trapezitergum grande*, Yu, Ślipiński & Shih, 2013; ventral view of holotype; CNU-COL-NN-2010-411. **B:** *Trapezitergum grande*; overlay drawing with anatomic structures; CNU-COL-NN-2010-411. Three buprestid species (C–F) that occur in the latest Middle Jurassic Jiulongshan Formation at the Ningcheng Locality, Inner Mongolia Autonomous Region, China, demonstrating an earlier presence of this family in northeastern China (PAN et al. 2011). **C:** *Sinoparathyrea gracilentata* Pan, Chang, Ren & Shih, 2011; dorsal view of holotype, part; CNU-COL-NN-2010-407P. **D:** *Sinoparathyrea bimaculata* Pan, Chang Ren & Shih, 2011; ventral view of holotype; CNU-COL-NN-2010-408. **E:** *Sinoparathyrea robusta* Pan, Chang, Ren & Shih, 2011; dorsal view of holotype (counterpart); CNU-COL-NN2010-410C. **F:** *Sinoparathyrea robusta* Pan, Chang, Ren & Shih, 2011, ventral view of holotype (part); CNU-COL-NN2010-410P. Fig. 6A–F reproduced with permission from Magnolia Press. (Scale bar: 1 mm)



for two and probably three DTs. This damage-type suite is linked to the same herbivore insect species, but represents different feeding interactions, or DTs (LABANDEIRA et al. 2007), produced from multiple developmental stages, such as larvae and adults, or from different tissue-accessing insect organs such as mouthparts for feeding and ovipositors for inserting eggs into plant tissues. From careful documentation and examination of links among insect DTs, particularly those on the same plant host, the damage-type suite can serve as a guide to how different feeding and ovipositional damage is controlled by insect ontogenetic development.

A recent study of herbivory in Panamanian forest canopies examined the pattern of disparate plant damage allocated to different DTs but created by the same insect species (CARVALHO et al. 2014). For external foliage feeders, damage was inflicted on plants by monodamagers, insects responsible for producing a single DT on foliage from feeding or ovipositing. Multidamagers were those insects responsible for multiple DTs on foliage. Recognition of modern feeding resulting in a distinctive DT involved identification of the culprit insect herbivores by rearing insects in the laboratory, photodocumentation of insects caught in the act of feeding on their plant host at night, and reference to the extensive agricultural, forestry and entomological literature. In certain circumstances in the fossil record, multidamager insects may be determined by very careful documentation of plant damage and by observing linkages between DTs, such as the *F. offae* leaf mine (DT280), adjacent interveinal oviposition marks (DT101), and nearby surface feeding (DT103).

6.2. Preangiospermous and angiospermous leaf-mining phases

One of the most profound events relevant to this discovery was the angiosperm radiation during the mid Cretaceous from ca. 125 to 90 Ma that, with few exceptions, provided a near-global replacement of gymnosperm-dominated floras by angiosperm floras (FRIIS et al. 2011). This worldwide floral replacement occurred during a 35 million-year-long interval (FRIIS et al. 2011). The occurrence of *Fossafolia offae* on *Liaoningocladus boii* during the mid Early Cretaceous of this interval is one of many examples of insect herbivore and pollinator interactions (REN et al. 2009; LABANDEIRA 2014a,b) that represent an older phase, commencing before the mid-Cretaceous, of insect interactions with gymnosperms (and ferns). This older phase contrasts with subsequent interactions involving angiosperm hosts initiated by the angiosperm radiation (LABANDEIRA 2006a, 2014a,b; REN et al. 2009). One of these types of interactions that preceded the angiosperm radiation included leaf mines on broadleaved, parallel-veined and entire-margined leaves of multiple lineages of gymnosperms (including conifers) – a type

of interaction occurring throughout the earlier Mesozoic (ROZEFELDS & SOBBE 1987; ZHERIKHIN 2002; SCOTT et al. 2004; LABANDEIRA 2006a; MELLER et al. 2011).

Similar leaf mines also are found on broadly similar conifer leaves in more recent taxa (WISE 1962; WEIDLICH 1986; DUGDALE 1996; MARTIN 2000). The occurrence of these extant leaf-mining associations suggests that modern leaf-miners of broadleaved conifer foliage may: (1) have antecedents that colonized gymnosperm hosts extending earlier into the Mesozoic and antedating the mid Cretaceous, or (2) alternatively may have colonized more recent gymnosperm hosts after angiosperm diversification during the Late Cretaceous to present (LABANDEIRA 2014a). Nevertheless, it appears that the Coleoptera were dominant leaf miners on broadleaved conifers in pre-angiospermous, mid-Mesozoic floras (SCOTT et al. 2004; MELLER et al. 2011), as possibly were “symphytan” Hymenoptera (FROST 1924; HEITLAND & PSCHORN-WALCHER 1993). Interestingly, Lepidoptera are the most common leaf miners of extant, broadleaved conifers (WISE 1962; DUGDALE 1996), a dominance that may have extended to the initial diversification of angiosperms during the mid-Cretaceous (LABANDEIRA et al. 1994; SOHN et al. 2012), during which there may have been competitive displacement of earlier colonizing beetle leaf-mining lineages.

7. Conclusions

There are four principal results of this study which include implications for future study of plant-insect interactions, particularly of the mid Mesozoic in general and the Early Cretaceous of northeastern China in particular.

1. *A mid Early Cretaceous leaf mine and its taxonomic affiliation.* A mid-Cretaceous leaf miner, assigned to damage type DT280, is formally erected as *Fossafolia offae* nov. ichnogen. et nov. ichnosp. Ding, Labandeira & Ren. This mine type, based on a variety of evidence, is attributable to a beetle as the fabricator, and is most parsimoniously affiliated with the Buprestidae (metallic wood-boring beetles), likely a member of the Tribe Trachyini. The Trachyini includes the modern leaf-mining *Pachyschelus*, which produces a mine very similar to *Fossafolia offae*, now established as the oldest identified beetle mine in the fossil record.

2. *The damage-type suite concept.* On rare occasions there has been evidence for recognizing two or more diagnostic DTs of the same damage-inflicting insect. More formal recognition of this categorization now has been extended to the fossil record, related in part to current tree-canopy herbivory research. It is now realized that multidamager insects – or insects causing multiple DTs on their plant hosts – should be taken into account in the fossil record to more fully understand insect damage diversity in the past.

3. *Circumscribing identification of fossil leaf mines.* There are three fundamental and accessible ways to eval-

uate which potential, insect lineages may have caused a specified type of damage in the fossil record. These three methods provide an objective procedure for ferreting out a likely culprit lineage that caused distinctive, stereotyped damage patterns on fossil plant hosts. It is hoped that the proposed methodology can be further amplified to ensure a better method for circumscribing the fabricators of insect damage in the fossil record.

4. *Preangiospermous versus angiospermous plant-insect interactions.* The discovery of a beetle mine in the 125-million-year-old Yixian Formation is another example that documents the persistence of an earlier phase of gymnosperm-dominated interactions at the beginning of the angiosperm ecological expansion. *Fossafolia offae* is likely a preangiospermous interaction that became extinct and was supplanted by newly evolving clades, such as early lepidopteran lineages whose principal hosts were basal dicot angiosperms.

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Table ES1. The Eurasian Mesozoic Fossil Record of Buprestid Beetles. Our listing of Buprestidae is as complete as possible. The cited taxa were retrieved as searches from the online Paleobiology Database and our personal databases and collections. Unreliable affiliations from the older literature have been systematically excluded. Column ‘Age’: From oldest (top) to youngest (bottom).

<u>Location</u>	<u>Formation</u>	<u>Age</u>	<u>Taxa</u>	<u>Reference</u>
Russia, Nizhegorodskaya Oblast (Borehole 68)	[not mentioned]	Jurassic: Bathonian	<i>Ancestrimorpha volgensis</i>	ALEXEEV 1993
China, Inner Mongolia Prov. (Daohugou locality)	Jiulongshan	Jurassic: Late Callovian	<i>Sinoparathyrea bimaculata</i> , <i>Sinoparathyrea gracilenta</i> , <i>Sinoparathyrea robusta</i>	PAN et al. 2011
Kazakhstan, Chimkent Oblast (Mikhailkovka locality)	Karabastau	Jurassic: Oxfordian	<i>Acmaeoderimorpha ignota</i> , <i>Jurabuprestis karatauensis</i> , <i>Karatausia maculata</i> , <i>Metabuprestium ovale</i> , <i>Parathyrea jurassica</i>	ALEXEEV 1993, 1995, 2000
Germany, Bavaria (Eichstätt locality)	Solnhofen	Jurassic: Tithonian	<i>Pseudothyrea oppenheimeri</i>	ALEXEEV 1999
Mongolia, Kobdo Aimak (Myangad locality)	Gurvan-Eren	Cretaceous: Berriasian	<i>Planocoleus mjangadiensis</i>	PONOMARENKO 1986
Spain, Lérida Prov. (Rubies Quarry)	Caliza con Caraceas	Cretaceous: Berriasian – Valanginian	<i>Pseudochrysobothris ballae</i> , Buprestidae gen. et sp. indet.	WHALLEY & JARZEMBOWSKI 1985
Mongolia, Dundgov’ Aimak (Shin-Khuduk locality)	Shin-Khuduk	Cretaceous: Berriasian – Valanginian	<i>Mongolobuprestis gratioisus</i> , <i>Pseudomongoligena schinkhukense</i>	ALEXEEV 2000
China, Shandong (Shanwang locality)	Laiyang	Cretaceous: Late Hauterivian – Early Barremian	<i>Macronotus tuanwangensis</i>	HONG & WANG 1990
Russia, Transbaikalia (Semyon locality)	Zaza	Cretaceous: Hauterivian	<i>Acmaeoderimorpha? emersa</i> , <i>Cretothyrea optanda</i> , <i>Metabuprestium latipenne</i>	ARNOLDI et al. 1977, ALEXEEV 1996

Russia, Transbaikalia (Baissa locality)	Zaza	Cretaceous: Hauterivian	<i>Metabuprestium bayssense</i> , <i>Metabuprestium furcatorugosum</i> , <i>Metabuprestium latipenne</i> , <i>Metabuprestium shartologoiense</i> , <i>Metabuprestium vitimense</i>	ALEXEEV 1995, 1996, 1999
Mongolia Uverkhangai Aimak (Anda Khuduk locality)	Anda-Khuduk	Cretaceous: Hauterivian – Barremian	<i>Andakhudukia ponomarenkoi</i>	ALEXEEV 2008
China, Inner Mongolia (Liutiaogou locality)	Yixian	Cretaceous: latest Barremian	<i>Trapezitergum grande</i>	YU et al. 2013
China, Liaoning (Beipiao City locality)	Yixian	Cretaceous latest Barremian	<i>Mongoligenula altilabdominus</i> <i>Mongoligenula gracilis</i>	YU et al. 2014
Mongolia, Bayan Khongorskiy Aimak (Bon Tsagan locality)	Khuriltskaya	Cretaceous: Aptian	<i>Brevista zherichini</i> , <i>Crassisoma indistinctum</i> , <i>Diceromorpha</i> , <i>longipennis</i> , <i>Elegantella pono- marenkoi</i> , <i>Metabuprestium bontsaganense</i> , <i>Metabuprestium cretaceum</i> , <i>Metabuprestium dundulense</i> , <i>Metabuprestium granulipenne</i> , <i>Metabuprestium minutum</i> , <i>Metabuprestium nobile</i> , <i>Mongoligena curia</i> , <i>Mongolo- buprestis graciosus</i> , <i>Mongoligena vulgata</i> , <i>Paleas maculipennis</i> , <i>Paramongoligena transversicollis</i> , <i>Stigmoderimorpha rasnitsyni</i> <i>Umerata mirabilis</i> , Buprestidae incertae sedis	ALEXEEV 1993, 1995
Russia, Yakutiya (Sakha locality)	Eksenya-Khaya	Cretaceous: Aptian	<i>Metabuprestium oyunchaiense</i>	ALEXEEV 2000
Mongolia, East Aimak (Shar Tologoy locality)	Shar-Tolgoy	Cretaceous: Aptian	<i>Metabuprestium dundulense</i> , <i>Metabuprestium granulipenne</i> , <i>Metabuprestium ichbogdoense</i> , <i>Metabuprestium shartologoiense</i>	ALEXEEV 1995, 2009
Russia, Khabarovsk (Khetana River locality)	Emanra	Cretaceous: Middle Aptian	<i>Cretalbiana major</i> , <i>Cretalbiana sukatshevae</i>	ALEXEEV 2013

Myanmar, Kachin Prov. (Burmese amber)	?Taungbwet Taung	Cretaceous: earliest Cenomanian	<i>Acmaeodera burmitina</i>	COCKERELL 1917
Kazakhstan, Chiment (Kyzl-Dzhar locality)	Beleuty	Cretaceous Turonian	<i>Cretofrontolina kyzldzharica</i> <i>Kyzlordynia obscura</i>	ALEXEEV 2009
Russia, Yakutia (Arkagala locality)	Arkagalinskaya	Cretaceous: Turonian	<i>Metabuprestium arkharensense</i> , <i>Metabuprestium sibiricum</i>	ALEXEEV 2009

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